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THE LOWER PERMIAN INSECTS OF KANSAS. PART 6.

Delopteridae, Protelytroptera, Plectoptera and a New Collection of Protodonata, Odonata, Megasecoptera, Homoptera, and Psocoptera.

By Frank M. Carpenter.

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Delopteridae, Protelytroptera, Plectoptera and a New Collection of Protodonata, Odonata, Megasecoptera, Homoptera, and Psocoptera.*

By Frank M. Carpenter.

During the summer and fall of 1932, since the previous part of this series of papers was sent to the press, the writer was enabled by a grant from the Milton Fund of Harvard University to make an extensive trip to the central and western parts of the United States for the purpose of collecting fossil insects. One of the formations investigated was the Lower Permian limestone at Elmo, Kansas, where about two thousand specimens were obtained, bringing the total number of insects in the Harvard collection from this locality to some forty-three hundred.

Most of this new material, however, was collected in a layer of limestone which has not previously been worked for insects. The layer was first found during the summer of 1931 by Mr. C. B. Read, of the United States Geological Survey, who very kindly furnished me with a complete description of its position. It is exposed in a short gully running from east to west about four hundred feet northwest of the quarry which yielded the Harvard collection of 1927 (see plate 1 of Part 1 of this series of papers, 1930). With the exception of this new limestone bed the stratigraphy here is essentially the same as indicated by Dunbar in his diagrammatic section of the region (1924). In figure 1, plate 1, I have included a photograph of part of the 1932 quarry, showing the position of the new layer in relation to the rest of the Elmo limestone. The floor of this quarry is the top of the stump layer (D). Resting upon this floor is the white, blocky limestone (C) which at other exposures has produced the insects comprising the Sellards, Yale, and earlier Harvard collections. This layer is exposed in small gullies scattered irregularly over about ten acres, although it is not everywhere fossiliferous. In all these other gullies this blocky layer of limestone is overlain by several feet of

* This series of studies has been aided by a Sheldon Traveling Fellowship from Harvard University, three National Research Fellowships, and by grants from the Carnegie Foundation, the Bache Fund of the National Academy of Sciences, and the Milton Fund of Harvard University.

shaly, thin-bedded limestone, unfossiliferous except for fragments of plants, as indicated in Dunbar's diagram of this area. But in the 1932 gully, shown on plate 1, this blocky layer is surmounted by about two inches of soft calcareous shale (B), which in turn is overlain by another blocky layer of limestone (A), the one found by Mr. Read. Above this is the shaly limestone found elsewhere in the field.

The new layer of limestone is apparently not very extensive. At the head of the gully (the part shown in fig. 1, pl. 1), the layer is best developed, but it is not very fossiliferous there. On the south side of the gully (the right of figure 1), the layer is well developed and most fossiliferous; I worked it back to about ten feet from the edge of the gully, at which point it became thin and much fractured. On the bank opposite the mouth of the gully, not more than twenty-five feet west of the exposure shown in figure 1, the layer is completely absent, its place being taken by the usual shaly limestone. On the north side of the gully (left side of figure 1), not more than eight feet from the opposite side, the layer disappears abruptly, apparently because of a fault with a throw of about eight feet, the bottom of the stump layer being as the level of the surface of the ground. Just how far the layer extends eastward, i. e., in the direction in which the photograph in figure 1 was taken, I did not definitely ascertain. About ten feet eastward, where I made a small section, the layer was absent, but it may be present a few feet either side of this spot. Even with this uncertainty, however, it is clear that the layer is decidedly lenticular and limited to a very small area in comparison with that covered by the rest of the Elmo limestone.

The new layer of limestone closely resembles the lower, but differs in certain particulars. It is much harder, requiring the use of a heavy hammer to break it up; at the blow of the hammer sparks are frequently seen and there is a noticeable odor of sulfur. The rock is also somewhat heavier than that of the lower bed, the average specific gravity of the upper layer being about twelve per cent higher than that of the lower bed. Finally, the mineralogical nature of the two layers is somewhat different. The new one contains spots of limonite and numerous dendrites of combined limonite and manganese oxide, the resultant compound being dark gray in color. These dendrites are so abundant in the rock that they are visible in nearly every fragment of the upper limestone. This provides a means of recognizing fragments of the layer, if they should happen to become mixed with pieces of the lower layer.

Although it is impossible to set a definite figure for the amount of time which elapsed between the deposition of the lower layer and the upper layer, I believe that we are justified in concluding that at the most this could not have been more than a few hundred years, which from a geological viewpoint means that the faunas contained in the two layers of rock were practically contemporaneous. But what is also significant is that these two layers of limestone are separated by a dissimilar type of rock,—unfossiliferous and of a different structure. Such a condition suggests a change in the environment, possibly of a climatic nature. This is also indicated by the differences in the two limestone layers, already mentioned above. In view of these facts we would be justified in expecting to find the faunas of the two layers somewhat different, for although the species in each layer might easily have existed during the several hundred years consumed in the deposition of the two layers, the environments were apparently not entirely alike. It was with the hope of finding this to be the case that I made plans to visit the Elmo locality again after Mr. Read had described to me this new limestone. As the field work progressed, it soon became evident that there was a noticeable difference in the composition of the faunas of the two layers. These differences cannot be adequately discussed until all species of both layers have been studied; but a general idea can be formed from the descriptions of the fossils contained in this paper, as well as from the relative abundance of the specimens belonging to the different orders as observed in the field. Since the two layers of limestone were so close together, as shown in the photograph on plate 1, the fossils of both of the beds were collected, which enabled an easy comparison of the faunas by the general run of the specimens. Mecoptera, Protoperlaria, and Plectoptera were much less abundant in the upper layer than in the lower, whereas Psocoptera and Homoptera were decidedly more numerous. Most significant of all, perhaps, is the fact that larvae and nymphs were much more abundant in the upper layer. My examination of these new fossils under considerable magnification shows that the body structures of the insects in the upper layer are much better preserved than those in the lower layer, as will be apparent from the descriptions of the fossils in this paper. Since most of the species, of some groups at least, occur in both layers, this fine preservation of the body has enabled us to determine for the first time the complete structure of many of these Permian insects.

In this paper I have taken up first the new fossils belonging to

groups which I have already treated in earlier publications devoted to the 1927 material, namely, the Protodonata, Odonata, Megasecoptera, Homoptera and Psocoptera; and following these, I have considered all the fossils in the Sellards and both Harvard collections belonging to the Delopteridae, Protelytroptera, and Plectoptera. In the descriptions of the insects of the Elmo limestone which are contained in this paper and others to follow, the layer which produced the specimens under discussion will be indicated as upper or lower, in reference to the new and old layers of limestone respectively. This will enable us to form an accurate conception of the two faunas when the study has been completed. Of course the Sellards, Yale and 1927 Harvard collections were taken entirely from the lower layer.

Before closing these introductory remarks, I wish to acknowledge the financial aid of the Milton Fund of Harvard University, which made the collection of this additional material possible; and the indispensible assistance of my wife, who collected with me in the field regardless of the difficult conditions, and secured about half of the series of specimens. We are both indebted to Mr. and Mrs. E. E. Bert and Miss Rowena Bert, of Abilene, Kansas, for the kindness which made our stay in Kansas pleasant in spite of the labor of the field work. We are also under obligation to Paul and Joseph Bert, who frequently helped us in the field and found several fine fossils. To Mr. C. B. Read, I owe my deepest thanks for furnishing me with notes concerning the new layer of limestone; and I am sure that all who are interested in the geological history of the insects share this gratitude with me.

Order PROTODONATA.

Seventeen specimens belonging to this order were collected in 1932, but three of these are small fragments which are too incomplete for determination. One other fragment (No. 3255), found in the lower layer of limestone, is so unusual that I have included a figure of it here (fig. 3), although there is not enough of the fossil preserved to justify the erection of a new genus and species. The preserved portion is 35 mm. long and consists of the anterior part of the wing near the apex. Judging from the size of the fragment, I estimate that the whole wing would be a little smaller than that of *Typus permianus,* probably around 10 cm. The peculiar features of the wing are the thickening of R1 in the region that would correspond to the pterostigmal area of the true Odonata, and the abnormal cell-formation be-

low this thickening. Nothing of this nature has been found in the described Protodonata, so in all probability the fossil represents a new family. It is very unfortunate that more of this strange wing is not preserved. Another fragment of a wing (No. 3256), collected in the upper layer of limestone, belongs to *Oligotypus tillyardi* Carp., which has previously been known only from the type; it consists of the middle portion of the wing. The remaining specimens of Protodonata, except the two described below, belong to *Typus permianus* Sellards, which is now so well known that these additional fossils require no further comment.

Family MEGANEURIDAE.

Typus readi, new species.

Figure 1.

Length of preserved part of wing, 102 mm.; maximum width, 32 mm. Sc extending well beyond the origin of Rs, probably to the apex

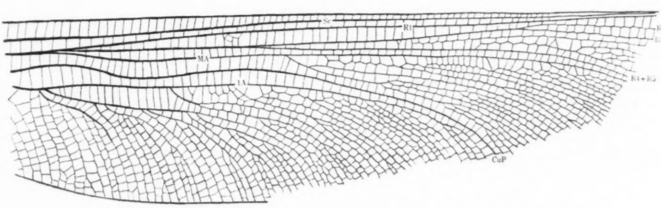

FIGURE 1. *Typus readi*, n. sp., holotype, No 3253ab, Mus. Comp. Zoology.

of the wing; R1 close to Sc distally, almost touching it beyond the origin of R3; R4 + 5 originating somewhat before the middle of the wing, remote from R3 and separated from it by several rows of cellules; first branch of MA arising slightly distad of the origin of Rs, Cu1 terminating beyond the middle of the wing; 1A well developed, remote from the hind margin; anal crossing undeveloped.

Holotype: No. 3253, Museum of Comparative Zoology; collected by the writer with the aid of Joseph Bert, in the upper layer of the limestone at Elmo. I have named this species for Mr. C. B. Read, of the United States Geological Survey.

This species is much larger than the genotype, *permianus* Sellards. Comparing the preserved part of *readi* with the corresponding portion of *permianus*, I estimate the whole wing of the former to be about

140–150 mm. long, that of *permianus* being only about 110 mm. long. This new fossil possesses many interesting characteristics which require us to modify our definition of the genus Typus in at least one respect. The subcosta of *readi* extends very nearly to the apex of the wing, if not actually to the apex, as in Megatypus; whereas in *permianus* it terminates near the middle of the wing. I do not believe that this difference is sufficient to justify the separation of *readi* into a distinct genus, since in other respects the venation is very similar to that of *permianus*. There is no specialized anal crossing at the base of the wing, as in Megatypus, and R4 + 5 originates at about the middle of the wing, not in the more distal portion as in Megatypus.

Megatypus vetustus, new species.

Figure 2.

Length of preserved portion of wing, 60 mm.; width, 20 mm. Sc terminating somewhat before the apex; R1 close to the anterior margin

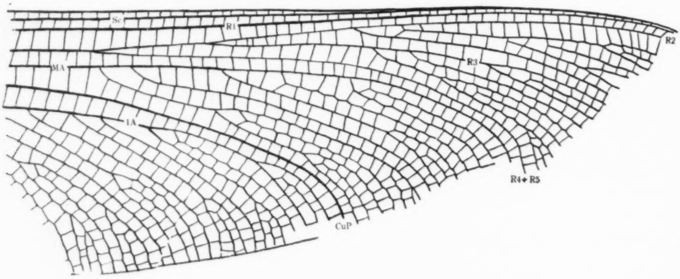

FIGURE 2. *Megatypus vetustus*, n. sp., holotype, No. 3254ab, Mus. Comp. Zoology.

distally; R4 + 5 arising well beyond the middle of the wing; first branch of MA originating just before the origin of Rs.

Holotype: No. 3254, Museum of Comparative Zoology; collected by the writer in the upper layer of the limestone at Elmo. This fossil consists of the distal half of a finely preserved wing, but there is enough to show definitely what its affinities are. The wing is much smaller than that of *schucherti*, for the size of the preserved part indicates that the whole wing would be about 110–115 mm. long, about 60 mm. shorter than that of *schucherti*. The late origin of R4 + 5, much be-

yond the middle of the wing, places the insect in Megatypus, even though the structure of the anal crossing is not known. The wing differs from that of *schucherti* in two obvious features: the subcosta terminates before the apex, and the first branch of MA originates proximad of the origin of Rs.

Before leaving the Protodonata, I wish to call attention to Martynov's recent paper (1932a) on the Meganeuridae, in which he proposes to separate this family into a distinct order, Meganisoptera. This order he distinguishes from the true Protodonata, as represented by Protagrion, by the difference in the structure of the cubitus. For he considers that MP in the Meganeuridae became attached to MA and degnerated into one or more of the pectinate branches of MA; also that the convex vein CuA (or Cu1) changed to a concave vein, and is

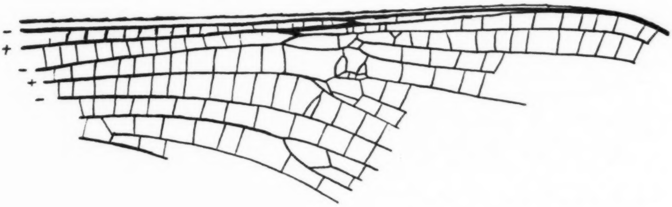

FIGURE 3. Fragment of wing of Protodonatan (No. 3255ab) in Mus. Comp. Zoology.

therefore the vein usually regarded as CuP (or Cu2). Similarly, the vein CuP (Cu2), which was originally concave, became convex and is hence the vein ordinarily identified as 1A. In a subsequent paper (1932b), however, after considering my description of the Protodonata in the Museum of Comparative Zoology, Martynov revises his conclusions and accepts the usual view that the convex and concave veins mentioned are CuA and CuP respectively. He still regards the Meganeuridae as a distinct order, though admitting that there is little to support this contention.

Order ODONATA.

Three specimens of Odonata were found in 1932, two of which belong to the Protozygoptera, while the third represents the Protanisoptera.

Suborder PROTOZYGOPTERA.

Family KENNEDYIDAE.

Kennedya mirabilis Tillyard.

Tillyard, 1925, Amer. Journ. Sci., **10:** 66; figs. 10–12.
Carpenter, 1931, Amer. Journ. Sci., **21:** 116; fig. 4.

One specimen of this species (No. 3220), found in the upper layer of limestone, consists of the basal two-thirds of a wing, from the very base to a little beyond the origin of IR3. The preserved portion of the wing is 17 mm. long and 4 mm. wide, so the whole wing would probably be about the same size as the type. This is the only specimen of *mirabilis* which has been found in addition to the types and it is the first one to show the cubitus and 1A complete. These veins were partly missing in the types (Nos. 5005, 5006a, Peabody Museum), but were assumed by Tillyard to be similar to those of Permagrion, from the Australian Permian. This new fossil shows that Cu2 and 1A were essentially as he supposed them to be. 1A extends to a point nearly below the origin of R3, sending a series of eight veinlets to the posterior margin.

There are a few points of difference between the new fossil and the types, but I believe that these are either only of an individual nature or are due to normal differences between fore and hind wings. The subcosta is longer in the new fossil, extending almost to the point of origin of R4 + 5. Also there is a cross-vein extending from R + M to Cu + 1A just basal of the origin of Rs + M which is not present in the types.

Progoneura minuta Carp.

Carpenter, 1931, Amer. Journ. Sci., **21:** 120–122; fig. 4.

The type specimen of this minute species consisted of the basal part of a wing. In the new material there is a nearly complete wing (No. 3221), found in the lower layer of limestone, which undoubtedly belongs to this species. The wing is somewhat smaller than that of the type, the preserved part (including all but the very apex of the wing) being only 15 mm. long. The entire wing could not have been more than 17 mm. long at the most and my estimate of the length of the type specimen was 21 mm. The new wing is also narrower than the type at the base, just beyond the petiole. But in Recent Zygoptera, at least in the Agrionid groups, the hind wings are noticeably shorter and narrower at the base than the fore wings, so that I

am led to believe that this new fossil is the hind wing of *minuta*. Aside from these differences in size and shape, the preserved part of *minuta* is identical with the corresponding part of the new wing.

Inasmuch as the fossil is more complete than the type we are now able to add to our knowledge of the specific features of this insect. The base of the wing has already been described in detail in the original description of the species (1931), so I shall confine my discussion to the parts of the wing now known for the first time. Unfortunately, the cross-veins are not clearly preserved and parts of the posterior margin are broken away. Two post-nodals are visible, one just beyond the end of Sc and the other at about the middle of the wing. The pterostigmal area is preserved, but the pterostigma itself is not discernible. Rs, as suggested even in the base of the wing of the holotype, is surprisingly remote from R1 for its entire length. This is one of the out-standing features of the wing and may rank as a generic characteristic. R4 + 5 originates slightly distad of the termination of Sc and it terminates on the posterior margin quite remote from the apex of the wing. MA, of course, also terminates on the posterior margin, just beyond the middle of the wing, at a point far more proximal than in Kennedya; and Cu2 apparently ends below the origin of R4 + 5, much nearer the base than in any of the other known Protozygoptera. The space between Cu2 and MA is very wide distally.

Suborder PROTANISOPTERA.

Family DITAXINEURIDAE.

Ditaxineura cellulosa, new species.

Figure 4.

Length of preserved part of wing, 15 mm.; width, 6 mm. Wing pointed; three cross-veins between R1 and R2 + 3; two cross-veins between R2 and the pterostigma; three cross-veins between the consecutive branches of Rs.

Holotype: No. 3222, Museum of Comparative Zoology; collected by the writer in the upper layer of the limestone at Elmo, 1932. The type consists of the distal half of a very clearly preserved wing.

This species, the second in the genus, is close to *anomalostigma* (see Carpenter, 1931, fig. 4), but is larger and possesses more cross-veins and consequently more cells. The corresponding part of the wing of *anomalostigma* is 11 mm. long; if the wing of *cellulosa* was the same shape as that of *anomalostigma,* and there is no evidence to the con-

trary, then the whole wing would have been about 28 mm. long, 7 mm. longer than that of *anomalostigma*. The difference in the arrangement of the cross-veins is rather striking. In *anomalostigma* there are only two cross-veins between the consecutive branches of Rs and between R4 + 5 and MA, whereas in *cellulosa* there are three in all cases. In the preserved part of *cellulosa* there are consequently 41 cells; whereas in the corresponding part of *anomalostigma* there are only 29 cells.

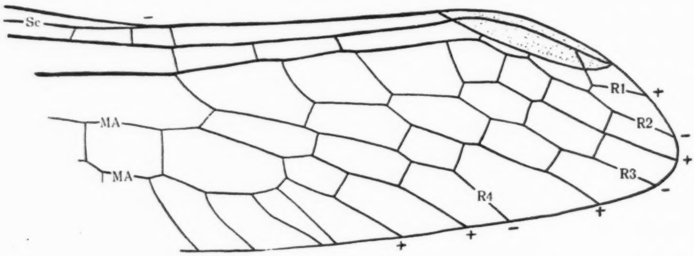

FIGURE 4. *Ditaxineura cellulosa*, n. sp., holotype, No. 3222ab, Mus. Comp. Zoology.

THE WING VENATION OF THE ODONATA.

Since the publication of my previous paper on the Lower Permian Odonata (1931), several additional accounts have appeared in print describing other Permian Odonata and discussing the evolution of the wing venation. Only a few weeks after the publication of my paper mentioned above, in which I established the suborder Protanisoptera, Martynov (1931a) published a description of a new fossil from the Permian of Russia, which he called Permaeschna. He assigned this genus to a new suborder, which he also named Protanisoptera, not knowing that I had already used this term. In a subsequent note (1931b), after discovering this repetition of names, Martynov substituted the term Permanisoptera for his Protanisoptera. In a still later paper (1932) he discussed more completely the relationship between Ditaxineura and Permaeschna and concluded that the two fossils and hence the suborders Protanisoptera and Permanisoptera were only remotely related and that whereas the Permanisoptera were the ancestors of the true Anisoptera, the Protanisoptera were an aberrant, side-branch. This conception of the affinities of these fossils is founded upon Martynov's interpretation of the venation of

the anisopterous forms, an interpretation which differs widely from that employed by Lameere, Tillyard, and others, as well as previously by Martynov himself.

Since Martynov's explanation of the venation of the Odonata is based mainly on his conception of the venation in Permaeschna, let us first examine the fossils belonging to this genus. Two such specimens have been found and they have been placed by Martynov in separate species, *dolloi* and *proxima.* The latter consists only of the very distal part of a much distorted wing, including the area between the apex and the base of the pterostigma. This specimen therefore reveals none of the important phylogenetic features of the wing and may be dismissed without further comment. *Dolloi* consists of a rather poorly preserved wing, lacking the entire basal portion including the arculus, and having the more distal part considerably distorted. Certain areas in the central part of the wing are broken away or are obscure. Now it can be seen from this account of the nature of the fossils that the most important area of the wing, the arculus region, on which the classification of the Odonata is chiefly based, is completely unknown, so that whatever conclusions one may reach on the affinities of these fossils can only be regarded as controvertible until the nature of the arculus region has been determined. So far as the veins present in the wing are concerned, Martynov believes that CuA and MP are present in addition to CuP and MA, which have usually been recognized. He contends that CuA, however, has lost its basal connection with the stem of Cu and arises from M near the middle of the wing; and that MP is a short vein arising more or less below the nodus. But since the base of the wing is missing, there is absolutely no evidence to support the idea that CuA has become attached to the stem of M. So far as the preserved portion of the wing is concerned, we have as many reasons for assuming that it has *not* fused with M as for assuming that it *has* fused, especially since no Odonata are known which show such fusion. And as for the distal branch of MA, there are no more reasons for regarding this as MP or any other longitudinal vein than there are for considering the other secondary veins (such as the radial supplement) to be derived from a main vein. Or to put the last idea differently, since secondary veins are known to exist in the wing of Permaeschna, then there seems to be no evidence indicating that the distal branch of MA is more than a secondary vein.

I am therefore led to believe that Martynov's interpretation of the venation of Permaeschna is without foundation, simply because the

important regions of the wing are not preserved, including the basal connection of the main veins. His conclusions may be correct, but at present there does not seem to me to be any evidence in this direction; and it is hardly justifiable to discard the now widely used interpretation of the venation in the Odonata without substantial proof.

About the same time that Martynov's description of Permaeschna appeared in print, Zalessky (1931a, 1931b) published a description of another odonate fossil, *Philidoptilon camense,* from a slightly different locality, but from the same horizon. He placed this fossil, which consisted of a single wing lacking the apex and most of the posterior part, in a new order, which he termed the Permodonata. From his description and discussion of this fossil it is at once obvious that Zalessky had only a very vague idea of the venation of the Odonata; he employs a somewhat modified form of the Comstockian system of nomenclature, assuming that the radial sector arises in the region of the nodus and crosses over part of the media. In a later paper (1932) Zalessky, apparently after investigating the literature on the venation of the Odonata, reconsiders the venation of Philidoptilon and proposes another interpretation of the evolution of the wings of the Odonata, as well as of the Plectoptera. Zalessky also advocates a new system of terminology for the veins, which is as confusing as it is misleading. He still contends in this second paper that Rs crosses over a part of the media, but he coins a set of new names for most of the other veins. He designates M1, M2, and M3 of Comstock (Rs of Lameere, Tillyard, etc.) as the *mediana anterior* (M. a.); M4 of Comstock as the *mediana posterior* (M. p.); a part of Comstock's Cu as the *cubitus anterior* (Cu. a.); and Cu2 of Comstock as the *cubitus posterior* (Cu. p.). As Zalessky himself has pointed out his *mediana anterior* is very different from the *anterior media* (MA) of Lameere, Tillyard, etc.; his *mediana posterior* different from the *posterior media* (MP) of Lameere; and so forth for the branches of the cubitus. It is difficult to understand why Zalessky, if he wished to coin new terms for these veins, should have employed ones which were identical in all but word order with those now in general use! In addition to the confusion caused by the use of such similar terminology much obscurity is thrown over Zalessky's arguments by the frequent occurrence of inaccurate and contradictory statements. He states that Redtenbacher and Brongniart designated concave veins by odd numbers and convex veins by even ones, although these authors actually did the reverse! Zalessky's paper on the venation of the Odonata is such a combination

of misunderstandings and inaccuracies that his whole discussion is valueless.

As Martynov has already pointed out (1932a, p. 36), the figure of Philidoptilon given by Zalessky shows that the fossil is not only a member of the order Odonata, but is referable to the suborder Protanisoptera. In fact, Ditaxineura and Philidoptilon are strikingly similar in all important features, especially in view of the fact that the latter specimen is considerably distorted. Philidoptilon has a larger number of cells than Ditaxineura and it may also have had a differently shaped pterostigma; Zalessky shows the latter just distal of the nodus, but this is so far from the apex of the wing and the structure of the pterostigma so unusual as drawn by him, that I suspect that the real pterostigma is beyond the preserved part of the wing. The anal area of Philidoptilon is of particular interest; by linear arrangement of the sides of certain cells, directly below 1A, a longitudinal vein is formed which becomes fairly straight towards the margin of the wing. Now if we compare this area of Philidoptilon with that of Permaeschna, bearing in mind the presence of this secondarily formed vein in the former, we note a very close resemblance. In fact it would not be at all difficult for us to imagine the basal part of the wing of Philidoptilon attached to the preserved part of *Permaeschna dolloi*. The concave vein which Martynov figured below 1A in the latter could easily be formed by the linear arrangement of the sides of certain cells, as indicated nearer the base in Philidoptilon. This of course is only a supposition and too much weight should not be attached to it; but I believe that when the whole wing of Permaeschna is found, it will be very similar to that of Philidoptilon and Ditaxineura.

Order MEGASECOPTERA.

Suborder PROTOHYMENOPTERA.

Twenty-seven specimens belonging to this group were collected in 1932, aside from fragments too small for further study. Although most of these fossils are members of the family Asthenohymenidae, some excellent Protohymenidae are also included, which have enabled us to obtain for the first time a definite conception of the general habitus and body structure of these remarkable insects.

Family PROTOHYMENIDAE.

Protohymen permianus Till.

Protohymen permianus Tillyard, 1924, Amer. Journ. Sci. (5) **8**: 114.
Tillyard, 1926, ibid., **11**: 58.
Carpenter, 1930, Psyche, **37**: 349; fig. 1, 11.

Two specimens (No. 3264ab and 3265ab, Mus. Comp. Zool.) were found in the lower layer of limestone, and another (No. 3261ab), consisting of the basal part of a wing, was taken in the upper layer. One of the former specimens (No. 3264) consists of a finely preserved hind wing and is the best wing of this insect which I have seen. The venation is very nearly the same as shown in figure 1 of my earlier paper (1930), but differs in three respects: MA separates from Rs immediately after contact with it; the first cross-vein between R4 + 5 and MA is missing; and there are two cross-veins between Cu1 and MP. These are undoubtedly only individual variations.

Protohymen elongatus Carp.

Protohymen elongatus Carpenter, 1930, Psyche, 37: 353; fig. 2.

This species was previously known only from the holotype, which lacked a small part of the wing below the pterostigma. In the new material there are two more specimens. One of these (No. 3263), found in the upper layer, consists of the distal part of a wing, finely preserved. This of course shows the area of the wing missing in the type; it is essentially as I had restored it in my figure, with the cross-veins distributed as in *permianus*. The preserved part of the wing is 8 mm. long, which indicates that the whole length of the wing was about 20 mm. long, the same size as the type. There is one venational feature of this specimen which does not occur in the type, although it is unquestionably an individual characteristic; MA coalesces with Rs close to the origin of the latter, so that the fused portions of these veins are much longer than in the type. This new specimen of *elongatus* is of considerable importance, because it has enabled us to ascertain the nature of the apical region of the wing and to distinguish between *elongatus* and the new species described below.

The second specimen of *elongatus* (No. 3262ab), also from the upper layer, consists of all four wings and the abdomen, including the cerci. Three of the wings are more or less twisted, but the fourth, a hind wing, is spread out flat, and although a part of the base is broken away, the wing is 18 mm. long. This specimen is most interesting

because of the preservation of the cerci, which have not previously been found in the Protohymenidae, although I have already described them in the Asthenohymenidae. The cerci, which are perfectly preserved, are 16 mm. long and are broken off at that length, so that in all probability they were some longer. There are about fifty segments in the preserved part of the cerci, shaped like those of *Asthenohymen dunbari*.

Protohymen readi, new species.

Figure 5.

Fore wing: length, 19 mm.; width, 3.5 mm.; very slender and pointed; R1 slightly diverging from the costal margin in the pterostigmal region, but the space between the costal margin and R1 is

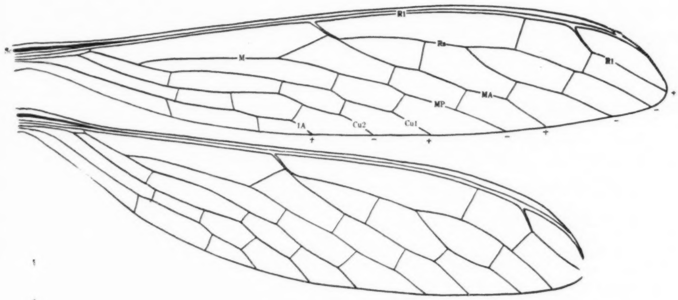

FIGURE 5. *Protohymen readi,* n. sp., fore and hind wings; holotype, No. 3257ab, Mus. Comp. Zoology.

uniformly thickened and chitinized; between R1 and R2 + 3, just proximal of the pterostigma, there is a long heavy cross-vein; the first cross-vein between R1 and MA is proximal of the fork of Rs; Cu1 diverges upwards after its separation from Cu2, and immediately coalesces with the stem of M; MP separates from Cu1 close to the base of the wing, before the first cross-vein between Cu1 and Cu2; there are three cross-veins between Cu1 and Cu2, and three between Cu2 and 1A; 1A is joined to the posterior margin by two cross-veins, one midway along 1A and the other just before its termination.

Hind wing: length, 17 mm.; width, 4 mm.; slender and pointed; venation similar to that of the fore wing, except that the pterostigmal cell is somewhat shorter.

Length of body, not including cerci, 19 mm.; width of thorax, 2.8 mm.

Holotype: No. 3257ab, Museum of Comparative Zoology; collected by the writer in the upper layer of limestone at Elmo, in 1932. This species is named for Mr. C. B. Read, of the United States Geological Survey.

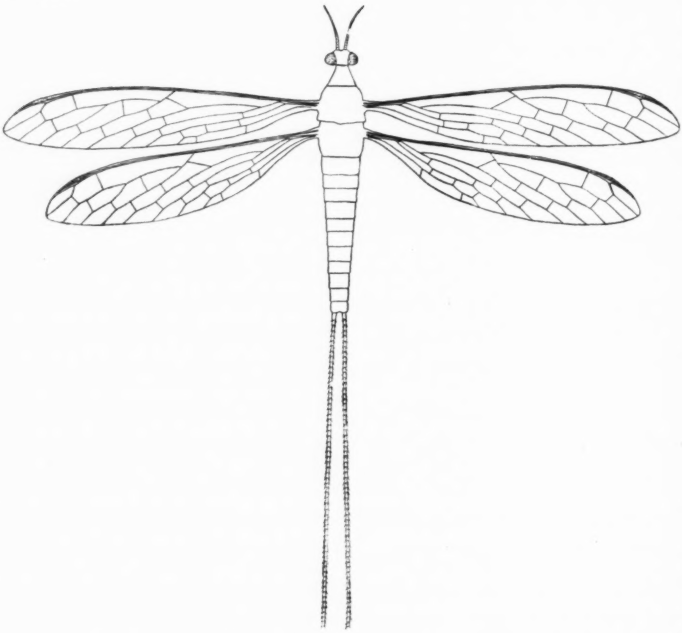

FIGURE 6. Reconstruction of *Protohymen readi*, n. sp., based on specimen No. 3257ab, with the addition of the cerci present in *Protohymen elongatus* Carp. (No. 3262ab). The legs are unknown.

This specimen consists of all four wings outspread, in a fine state of preservation, together with the head, thorax, and abdomen. Only the first few segments of the cerci are preserved, but undoubtedly the cerci were similar throughout all the Protohymenoptera. The antennae of this specimen are also preserved, but unfortunately the

segments are not clearly separated; in all probability the antennae of the Protohymenidae were much like those of the Asthenohymenidae, already described in detail. The head is rather broad and possesses large compound eyes, which appear in the fossil to project posteriorly slightly, though this may be due to the position of preservation. The prothorax, which is clearly preserved, is rather long and is narrowed anteriorly. The prothorax is thus very similar to that described by Martynov (1932) in Pseudohymen, from the Permian of Russia. The mesothorcic and metathoracic segments in *readi* are rather large in proportion to the rest of the body, but that may be due in part to the flattening of the body during preservation. The segmentation of the terminal part of the abdomen is somewhat obscure, but this again was probably more or less the same in all the members of the family.

The wings of *readi* resemble those of *elongatus* closely and to a smaller degree those of *permianus*. From both of these, however, they can be distinguished by the presence of the long cross-vein between R1 and R2 + 3 before the pterostigma, as well as by minor characteristics, such as the earlier branching of MP from Cu1, and the presence of the third cross-vein between Cu2 and 1A.

This specimen of *readi* is especially interesting because of certain resemblances to the Protohymenoptera which have recently been described by Martynov from the Permian of Russia (1932). Four species were found by him in these beds, two of which, *Pseudohymen angustipennis* Mart. and *Ivahymen constrictus* Mart., belong to the family Protohymenidae. The other two, *Kuloja paurovenosa* and *K. cubitalis* Mart., belong to a very different family, Kulojidae. In the wings of the specimens of Pseudohymen and Ivahymen there is one vein which is not present in any of the previously described Kansan fossils,—the long cross-vein between R2 + 3 and R1, just proximad of the pterostigma. But in the specimen of *readi* this cross-vein shows in both pairs of wings. In other respects also *readi* approaches Pseudohymen and Ivahymen more closely than any of the other Kansan Protohymenoptera. The most obvious difference between these two Russian genera and *readi* is the number and arrangement of minor cross-veins. It should be noted that many of these cross-veins which Martynov has figured are shown as broken lines, indicating that their presence is not altogether certain. I think that we may also conclude that other cross-veins may exist in the wings of the Russian fossils, such as between the hind margin and 1A, but are simply not

preserved. This lack of distinct preservation of the venation, as indicated by the broken lines in Martynov's figure of Pseudohymen may in fact account for his conclusion that M, Cu and 1A are coalesced with R1 at the base of the wing, which was the characteristic which he designated as the diagnostic feature of the genus Pseudohymen. If my suspicions are correct then in all probability Pseudohymen is much more closely related to *readi* and to the genus Protohymen than might be supposed at first from Martynov's figure. Certainly if the specimen of *Pseudohymen angustipennis* had been found in the Elmo limestone it would very likely have been placed in Protohymen; but naturally the remoteness of its real locality exaggerates the differences between these genera.

Since the type specimen of *angustipennis* has the body partially preserved, we are able to compare the body structure of this insect with that known in *readi.* Of particular interest is the similarity in the shape of the thorax, especially the prothorax, which is long and tapering in both insects. It is slightly longer in the Kansas fossil but the general form is remarkably close. The head and eyes are almost the same, although Martynov's fossil does not have the eyes shaped quite the same as in *readi.*[1] The abdomen is obviously much better preserved in the specimen of *angustipennis* than in that of *readi,* where it is curved to one side near the middle. The legs are not preserved in Martynov's fossils and only the femur of the right fore leg is visible in the type of *readi,* so we do not yet know anything of the leg structure of the Protohymenidae; but in all probability the legs of the members of this family were much the same as in the Asthenohymenidae, in which they have previously been described.

Family Asthenohymenidae.

Asthenohymen dunbari Till.

Asthenohymen dunbari Tillyard, 1924, Amer. Journ. Sci. (5) **8**: 117.
Doter minor Carpenter (nec Sellards), 1930, Psyche, **37**: 360; figs. 2, 12, 13, 14; plate 2.
Doter minor Carpenter, 1931, Amer. Journ. Sci. (5) **22**: 127; fig. 8.
Asthenohymen dunbari Carpenter, 1932, ibid., **24**: 21.

Six good wings of this species were taken in 1932, three of which came from the upper layer of limestone. None of these specimens

[1] Tillyard has described the eyes of *Permohymen schucherti* as being very small (1926, fig. 1), but I have been unable to discern them at all in the poorly preserved specimen which he figured.

consists of more than a single wing, however, so that we are not yet able to distinguish between the fore and hind wings. It does not appear possible to estimate these differences in the pairs of wings from those which are known to occur in the Protohymenidae, for in the latter the differences between the fore and hind wings are in shape and the wings of Asthenohymen are so unlike those of Protohymen and Permohymen in form that we are unable to assume similar differences.

In my former paper on the Protohymenoptera (1930) I included a figure of the wing of a specimen of *Asthenohymen dunbari* in which I indicated that the wing was very narrow at the base and that the anterior margin near the base bulged outward slightly. Among the new specimens I find an interesting series of modifications of these two features. In specimen No. 3266 and 3267, for example, the hind margin is more or less smoothly rounded basally so that the wings are not nearly so narrowed at the base as shown in my figure; in specimen No. 3269 the hind margin is also somewhat curved, but the wing is fully as narrow basally as indicated in my figure. In specimen No. 3268 there is a noticeable bulge in the hind margin but the base is not nearly so narrow as in the foregoing fossil. I am therefore led to the conclusion that either the variation in both of these features is due to individual instability, or the variation in one of them (i. e. either the narrowness of the base or the bulge in the posterior margin) is due to the difference in structure of the fore and hind wings. At any rate since the fossils show no fixed association of these two features, it is clear that the differences in shape are not of a specific nature.

The new material has also enabled me to distinguish a certain variation in the form of Cu2. In the figure mentioned above, I represented this vein as being smoothly curved, approaching Cu1 at the base, but diverging from it distally. It now appears that while this form of Cu2 does occur, it is an extreme condition and not nearly so frequent as where Cu2 is straight, as in the specimen shown in figure 12 of my 1930 paper.

Asthenohymen pusillus Tillyard

Figure 7.

Asthenohymen pusillus Tillyard, 1926, Amer. Journ. Sci. (5) **11**: 68; fig. 7.

Doter pusillus Carpenter, 1930, Psyche, **37**: 362.

Although a rare species in the lower layer of the limestone, only three specimens having been found in a total of about 6,000 fossils,

this insect is apparently not uncommon in the upper layer, 8 specimens having been taken in 1932. Since *pusillus* has not been correctly figured, I include here a drawing of the venation. The wing is smaller and broader than that of *dunbari*, and has several distinctive venational characteristics, such as the very short 1A, and the presence of only one cross-vein between MP and Cu1. Apparently there is a weak cross-vein between Cu2 and 1A.

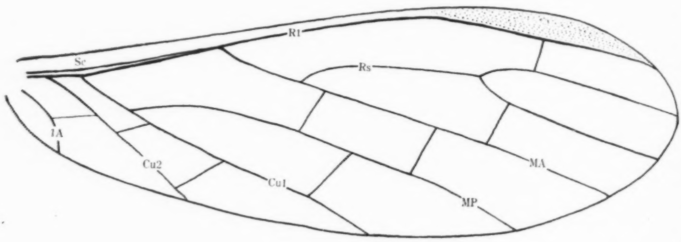

FIGURE 7. *Asthenohymen pusillus* Tillyard, fore(?) wing, based on specimens No. 3272ab and 3275ab, Mus. Comp. Zoology.

Asthenohymen affinis Tillyard.

Asthenohymen affinis Tillyard, 1926, Amer. Journ. Sci. (5) **11**: 65; fig. 2.
Asthenohymen stigmatazans Tillyard, ibid., 66; fig. 4.
Doter affinis Carpenter, 1930, Psyche, *37:* 361.
Asthenohymen affinis Carpenter, 1932, Amer. Journ. Sci. (5) **24**: 21.

This insect is also more abundant in the upper layer of limestone than in the lower layer, seven specimens having been collected there in 1932 and only three specimens having been found among all the fossils from the lower layer. Like *pusillus* this species has only one cross-vein between MP and Cu1, but it also lacks the basal cross-vein between Cu1 and Cu2 present in *pusillus*.

THE AFFINITIES OF THE PROTOHYMENOPTERA.

In my earlier discussion of the Protohymenoptera (1930) I concluded that the available evidence indicated that the Protohymenoptera were not ancestral to the Hymenoptera as originally advocated by Tillyard, but were merely a suborder of the Megasecoptera, which

apparently became extinct in the Permian without giving rise to any existing orders. This view of the affinities of the Protohymenoptera seems to be generally accepted,[2] although Tillyard asserts (1932, p. 23) that he cannot accept my "supposed proof of it." In this connection the new fossils, Pseudohymen and Ivahymen, described by Martynov from the Permian of Russia, and the specimens of Protohymen in the Harvard collection secured last summer are especially interesting since they serve to substantiate this widely recognized view. In figure 6 I have included a drawing of the whole specimen of *Protohymen readi*, n. sp., with the cerci added, as they are found in *Protohymen elongatus*. As already pointed out this insect bears a striking resemblance to *Pseudohymen angustipennis* Mart. and both approach closely the Carboniferous Megasecoptera. All the body structures which are known in the Protohymenidae, such as the head, thorax, abdomen, eyes, antennae and cerci are identical with those of the Megasecoptera. The similarity of the venation in the Protohymenoptera to that of the Megasecoptera has already been discussed in detail in connection with the 1927 Harvard collection, but *Ps. angustipennis* and *P. readi* approach the Carboniferous Megasecoptera in general form of wing even more closely than the previously known Protohymenoptera. Of course the wings of some species of the latter, as in Permohymen Tillyard, are much broader than those of the members of Protohymen and the Carboniferous Megasecoptera, but in these broad winged species the venation is identical with that of the extremely petiolate types, except of course for the distance between veins.

Although Megasecoptera are not uncommon in the European Carboniferous, only a very few specimens have been found in American rocks of that horizon and these are so aberrant that their assignment to the Megasecoptera has been very uncertain.[3] While I was first studying the Kansan Protohymenoptera in 1928 I was struck by the resemblance between the venation of these fossils and that of one of the aberrant megasecopterous forms, *Raphidiopsis diversipennis* Scudder (1893), from the Upper Carboniferous of Rhode Island. But there

[2] See for example Crampton, 1931, Ent. News, **42:** 136; Martynov, 1932, Trav. l'inst. Paléozool. de l'Acad. Sci. URSS, **1:** 2; Carpentier, 1932, Revue Quest. Sci., (4) **21:** 483.

[3] A typical Megasecopteron, belonging to the family Brodiidae, has recently been found in the Carboniferous of Kansas. The description of this insect is now in press.

were a few important points of difference in venation and not having the opportunity at the time to examine the type of Raphidiopsis at the National Museum, I made no reference to the fossil in my discussion of the Protohymenoptera. More recently, however, I had occasion to visit the National Museum and while there took advantage of the opportunity to study Scudder's fossil, which was kindly placed at my disposal by Dr. Bassler. Unfortunately the base of the fore wing is not preserved and the basal half of the hind wing is also obliterated; but I believe that enough is present to enable us to determine the relationship between this fossil and the Protohymenoptera. In figure 8 I have redrawn the fore wing of Raphidiopsis, and although the venation in general is the same as that given by Scudder, there are

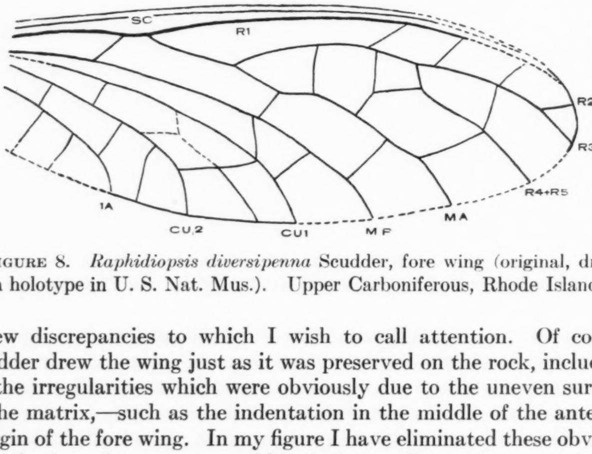

FIGURE 8. *Raphidiopsis diversipenna* Scudder, fore wing (original, drawn from holotype in U. S. Nat. Mus.). Upper Carboniferous, Rhode Island.

a few discrepancies to which I wish to call attention. Of course Scudder drew the wing just as it was preserved on the rock, including all the irregularities which were obviously due to the uneven surface of the matrix,—such as the indentation in the middle of the anterior margin of the fore wing. In my figure I have eliminated these obvious imperfections, just as one would omit from a figure of a recent insect such defects as wrinkles or tears in the wing. By completing the outline of the wing in this fashion, we find that the shape of the wing is more characteristic of the Megasecoptera than is suggested by Scudder's figure.

The subcosta can easily be recognized as a concave vein running more or less parallel to the costal margin and terminating in the apical third of the wing. Directly below the subcosta is the convex radius, which is more remote from the subcosta than the latter is from the

costal margin; just before the origin of Rs the radius bends downward slightly, but soon curves upwards again and continues to the apex, almost parallel to the anterior margin, without forking. Scudder was uncertain of the origin of Rs in the fore wing, as shown in his figure, where he connected it to the media by a broken line. But in the hind wing the origin of the radial sector is more clearly preserved and was correctly represented in his figure of that wing. In the fore wing also, I believe that this structure can be discerned with careful examination. At any rate, the venation of the fore and hind wings is known to have been the same in the Megasecoptera, so far as the main veins are concerned. It seems clear, then, that the radial sector originates directly from R near the middle of the fore wing,[4] and shortly gives rise to two main veins, the anterior one being the true radial sector and the posterior one the vein which I have designated MA. The radial sector itself divides into R2 + 3 and R4 + 5, the former forking slightly at its very tip. The media divides before the origin of Rs, according to my interpretation, into the anterior and posterior branches (MA and MP); MA is directed upwards and fuses with R, but the posterior media continues without branching to the hind margin. The oblique vein proximal to Rs, which I consider the stem of MA, was apparently not observed by Scudder, although it is very strongly preserved in the fore wing. The origin of the next vein (convex) is obscure; as far as it can be traced proximally it is independent of all other veins and its convexity and position shows that it is the first cubitus (Cu1). Between this vein and the next one proximal there is perhaps a short interpolated vein, which is very faintly indicated and seems to be formed by the alignment of two cross-veins; there is some doubt that this vein actually exists, for the wing in this region is almost obliterated. The next longitudinal vein, Cu2, is clearly preserved, except at the base; and the last vein which runs almost parallel to the inner margin of the wing is likewise distinct. The latter vein, of course, is one of the anals, presumably 1A. Since only one anal vein is usually all that is present in the Megasecoptera, it is fairly certain that no others existed nearer the base in the wing of Raphidiopsis.

A comparison of this wing with that of a more typical Megasecopteron, as Psilothorax, demonstrates clearly its close relationship to that order. In Psilothorax the forking of R2 + 3 is much deeper than

[4] According to my interpretation, of course, this stem of the radial sector really consists of Rs + MA.

in Raphidiopsis, and the longitudinal veins are closer together, especially in the apical part of the wing; but the most obvious difference lies in the fact that Rs arises far more distad in Raphidiopsis than it does in the other Megasecoptera, and that the origin of MA is more distinct. These are the features that set Raphidiopsis off from the more primitive and typical Megasecoptera, for which I have proposed the subordinal name Eumegasecoptera. Now if we also compare the wing of Raphidiopsis with that of the Protohymenoptera, as Protohymen, we shall note several interesting similarities. The subcosta and R1 are the same in both, except that they are more widely spaced in Raphidiopsis; and in the hind wing at least there is no pterostigma in that genus, although this structure is very weakly developed in Protohymen and Pseudohymen and consequently is not essential to the Protohymenoptera. R1 in Protohymen diverges away from the costal margin at the apex of the wing, a feature which is not found in Raphidiopsis; but it is also not found in Asthenohymen. The radial sector arises in the same manner in both insects; and, exclusive of the slight twigging of R2 + 3 in Raphidiopsis (which may be merely an individual feature) the branching of Rs is strikingly similar. Most interesting of all, perhaps, is the origin and formation of the anterior media (MA), including the oblique basal portion. In the Lower Permian Protohymenoptera this oblique vein joins Rs rather than R, as in Raphidiopsis; but the latter has the more primitive structure. The posterior media (MP) is the same in the two wings, although of course we do not know whether MP is independent or is fused with Cu1 at the base of the wing in Raphidiopsis. Cu2 and the anal veins of the latter are more like those of Permohymen than of Protohymen, because the subpetiolate wings of the members of Protohymen have naturally required a tenuity of the anal and cubital veins.

So close are the wings of Raphidiopsis and those of the Lower Permian Protohymenoptera that it is difficult for us to find points of variance. The suggestion of an interpolated vein between Cu1 and Cu2 in Raphidiopsis is the only difference that is particularly obvious. There are also more cross-veins in Raphidiopsis than in the Protohymenidae: 18 in Raphidiopsis and 10–14 in the Protohymenidae. Of course there may be some other differences in the base of the wing which are not preserved in Raphidiopsis; but it seems clear that this insect is more closely related to the Protohymenoptera than to the more typical Megasecoptera of the Carboniferous (Eumegasecoptera). In view of these facts I believe that Raphidiopsis should be regarded as a Carboniferous member of the Protohymenoptera.

Since the base of the wing of Raphidiopsis is not preserved, we are unable to determine whether or not it was petiolate or broad at the base. The Permian Protohymenoptera possessed both of these types of wing-form in the extreme, and it is interesting to note that the shape of the wings seems to have developed along similar lines in both the Protohymenidae and Asthenohymenidae. In the former family, the wings of Protohymen and Pseudohymen are petiolate, whereas those of Permohymen are very broad, especially at the base. In the Asthenohymenidae the wings of *Asthenohymen dunbari* are distinctly subpetiolate whereas those of *A. pusillus* are nearly as broad as in Permohymen. The shape of the wing, then, appears to have been a very minor factor in the evolution of the Protohymenoptera. In all probability the ancestral Carboniferous forerunner of the Protohymenoptera possessed subpetiolate wings, like most of the Carboniferous Megasecoptera. In connection with the broadening of the wings at the base, it is interesting to find that the fore and hind wings were not expanded to an equal degree. The Carboniferous Megasecoptera, so far as known, possessed homonomous wings, as did also Protohymen and Pseudohymen; whereas Permohymen had the hind wing much broader than the fore wing, especially in the region of the anal area. This was also probably true of *A. pusillus*. In both wings, however, the venation was the same, except for the space between the veins.

Returning to the question of the relationship between the Protohymenoptera and the existing insects, Tillyard has suggested (1932, p. 23) that if the Protohymenoptera are descended from the Megasecoptera, then we may have to reconsider the view originally proposed by Handlirsch that the Neuroptera were derived from them also. This suggestion of Tillyard's was made because of the presence of a certain insect, Martynoviella, in the Elmo limestone, which he considered to be neuropterous and to have a wing venation close to that of the Protohymenoptera. This question will be discussed fully in the account of the Neuroptera.

Order HEMIPTERA.

Over fifty specimens of Homoptera were collected in the Elmo limestone in 1932, about thirty being well preserved. Of this series of fifty fossils all but one (No. 3280, *Permopsylla americana* Till.) were found in the upper layer of the limestone. Since this is about twice as many Homoptera as have previously been found in the lower layer in

the Sellards, Yale, and 1927 Harvard collections combined, it is apparent that the order is more abundantly represented in the new limestone layer than in the lower one. The new material is as follows:

Lithoscytinidae, new family.

Tegmen: Sc parallel to R and R1, except at the base of the wing; R1 forked distally; M independent of R at the base of the wing; Cu dividing into Cu1 and Cu2 very near the base of the wing, *Cu1 continuing almost straight to the posterior margin, not fusing with M or even directed towards it;* Cu1 forked distally; Cu2 unbranched; 1A and 2A present.

Lithoscytina, new genus.

Tegmen: anterior margin straight or nearly so; R slightly arched at its base; M also arched at the base and parallel to R; Cu2 straight, remote from Cu1 distally; 1A remote from Cu2; 2A close to inner margin of the wing. Hind wing unknown.

Genotype: *Lithoscytina cubitalis*, n. sp.

Lithoscytina cubitalis, new species.

Figure 9.

Tegmen: length of preserved part (base to end of R1), 5 mm.; estimated length of whole tegmen, about 5.5 mm.; greatest width, 1.8 mm.; costal space relatively narrow; pterostigma slender; Rs originating at about mid-wing, at first directed posteriorly, but curving anteriorly near the apex; M dividing distad of the origin of Rs; Cu1 forked just before the division of M1; cell between Cu1a and Cu1b high; 1A terminating midway between Cu2 and 2A.

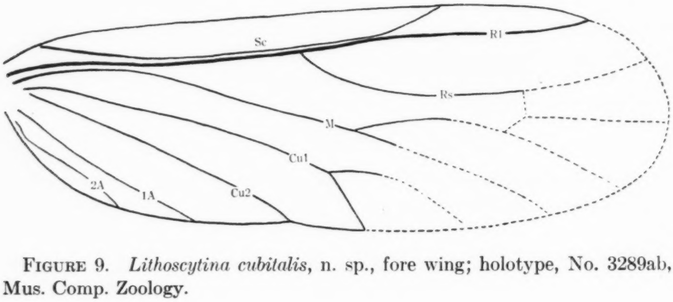

FIGURE 9. *Lithoscytina cubitalis*, n. sp., fore wing; holotype, No. 3289ab, Mus. Comp. Zoology.

Holotype: No. 3289, Museum of Comparative Zoology; collected by the writer in the upper layer of the limestone at Elmo, Kansas, 1932. The fossil lacks the apex and the distal part of the posterior margin; in figure 9 I have restored this part of the wing as it is in the Archescytinidae.

The family Lithoscytinidae is the third in the Homoptera now known from the Lower Permian of Kansas. The distinctive characteristic of this family is found in Cu1, which is free from M and not fused with it or even arched towards it as in all the other known species of Permian Homoptera. In this respect Lithoscytina is by far the most primitive Homopteron that has been found. The structure of the cubitus represents one more step towards the condition in the psocids. Aside from this peculiarity, Lithoscytina is similar to the Archescytinidae, except that 2A is much shorter and closer to the inner margin.

Family Archescytinidae.

Genus *Permopsylla* Tillyard.

Twenty-four specimens belonging to this genus were secured in 1932. Fifteen of these are too faintly preserved to show satisfactory specific characteristics, though in all probability they are either *permiana* or *americana*, the commonest species of the genus. Three tegmina of *americana* were found, of which No. 3282, taken in the upper layer of the limestone, is especially well preserved. In my earlier figure of this species (1931, fig. 3), I did not indicate the free piece of Cu1 basal of the junction with M because it was not clear in any of the specimens which had been found; but in this new fossil (No. 3282), as well as in another specimen (No. 3280, lower layer), this part of Cu1 is clearly preserved. It is essentially the same as in *permiana* (1931, fig. 4). The latter species is also represented in the new material from the upper layer by three tegmina, of which Nos. 3283 and 3284 are especially good. The following new species are also present:

Permopsylla grandis, new species.

Figure 10.

Tegmen: length, 6.5 mm.; width, 2.7 mm.; pterostigma short, R1b arched; R + M strongly arched at the base of the wing; Rs, after arising from R at a point nearer to the pterostigma than to the origin of M, curves posteriorly and then bends anteriorly near the apex of the wing, the arched formed being parallel to that of R1b; area be-

tween M and Rs very wide; M with three branches; M3 + 4 originating below the base of the pterostigma, remote from M2; distal cell of Cu1 about as high as long; 1A close to Cu2 and almost parallel to it; 2A remote from 1A and slightly sigmoidal in shape; inner margin of wing abruptly curved.

Holotype: No. 3287, Museum of Comparative Zoology; collected by the writer in the upper layer of limestone, 1932. This specimen is well preserved, showing all the veins clearly and lying smoothly on the rock. *Grandis* is much larger than any of the other described members of the genus and is also distinguished by the upward curvature of R1b and Rs.

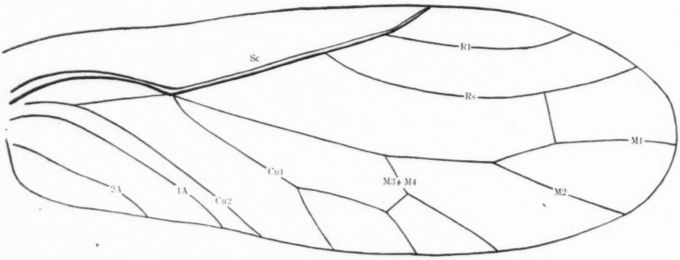

FIGURE 10. *Permopsylla grandis*, n. sp., fore wing; holotype, No. 3287ab, Mus. Comp. Zoology.

Permopsylla anomala, new species.

Figure 11.

Tegmen: length, 3 mm.; width, 1 mm.; pterostigma long; R1b slightly arched; Rs arising from R at a point much nearer to the origin of M than to the base of the pterostigma, the area between Rs and R1b being unusually wide; M with three branches; M1 diverging away from Rs distally; Cu1 with three branches, Cu1a apparently forked distally; cell between Cu1b and the lower branch of Cu1a about twice as high as broad; Cu2 smoothly curved; 1A close to Cu2 and converging towards it distally; 2A remote from 1A, slightly curved sigmoidally; inner angle of wing sharp.

Holotype: No. 3288, Museum of Comparative Zoology; collected by the writer in the upper layer of limestone at Elmo, 1932. The specimen is complete and shows the veins clearly.

Anomala is a very small species, being about the same size as *minuta* Carp. It is easily separated from the other species of Permopsylla by the presence of three branches on Cu1. It should be noted, however, that the extra branch may possibly be a part of the media, making the latter vein 4-branched; but the connection between this extra branch and Cu1 is very distinct, whereas that between it and M is very faint and is much like a cross-vein in appearance. Possibly the 3-branched condition of the cubitus may require the erection of a separate genus for this species. A 3-branched and even 4-branched cubitus has been found in other Permian Homoptera, however, as Orthoscytina, but has not been regarded as a generic characteristic.

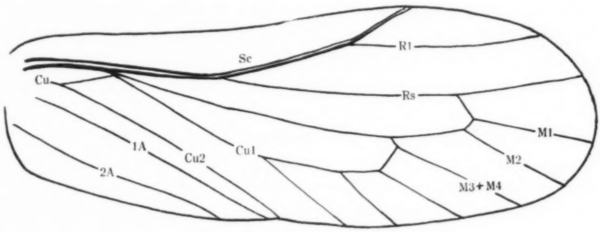

FIGURE 11. *Permopsylla anomala*, n. sp., fore wing; holotype, No. 3288ab, Mus. Comp. Zoology.

EVOLUTION OF THE HOMOPTERA.

Up to the present time a total of thirty genera of Homoptera have been described from the Permian, of which six are from the Kansas locality (Lower Permian), nine from Russia (Upper Permian) and fifteen from Australia (Upper Permian). Most of these fossils are known only from the tegmina; but the hind wings have been found in some of the Australian and Russian fossils. The body structure is known mainly from a single specimen of *Archescytina permiana* in the Museum of Comparative Zoology (Carpenter, 1931), although the general habitus of the body of an undetermined species of Scytinopteridae from Australia has been figured by Tillyard (1926). As I have already shown, the body structure of Archescytina demonstrates that the members of the family Archescytinidae, at least, cannot be referred to either the division Sternorrhyncha or Auchenorrhyncha,

but require a separate division which I called Paleorrhyncha. Whether the other Permian families of Homoptera, of which there are nine described, belong to this same division cannot be ascertained until various body structures, especially the antennae, are known.

From a comparison of the fore wings or tegmina of the Upper Permian and the Lower Permian Homoptera, I believe that we can form a fairly accurate idea of the evolution of the tegmina during this period of time, and perhaps reach some conclusions regarding the venation of the fore wings in the Carboniferous ancestor of the Homoptera. The tegmina of the Upper Permian Homoptera are more specialized than those of the Lower Permian species in the following respects:

1. The thickness and granulation of the membrane. That the membrane of the Lower Permian species was tough and heavy is indicated by the intensity of the convexity of R1, as well as by the apparent texture of the wing surface; but there is no sign of the granulation or pitting which is so clearly preserved in the Scytinopteridae of the Russian and Australian fossils.

2. The division of the tegmen into a tough basal part and a softer, delicate distal portion. The tegmina of some of the Prosbolidae[5] of the Upper Permian show a distinct division into these two parts, the dividing line extending from about the termination of R1a to the end of Cu1b. Correlated with this division is the formation of the break or bend in the smooth contour of the anterior margin, forming a nodus somewhat comparable to that of the Odonata. In none of the Lower Permian Homoptera is there an indication of such a nodal structure or of the division of the membrane.

3. The intensification of the claval suture. In the majority of the Upper Permian Homoptera the claval suture, which lies along Cu2, is very deeply cut so that most of the specimens lack the anal area, which has broken off along this suture. Although the latter is also present in the Lower Permian species, it is not very deep; I have not seen one specimen of the Homoptera from the Elmo limestone which had the anal area broken off along this suture.

The fact that none of the Lower Permian Homoptera lacked the specializations mentioned above led Tillyard to believe that the archetype of the Homoptera could be formulated from the characteristics of the family Archescytinidae. In most respects this view appears to

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[5] Regarded by Tillyard as directly ancestral to the Tropiduchidae and possibly to other families of the Fulgoroidea (Tillyard, 1926).

be correct, but the new fossil described above as *Lithoscytina cubitalis,* which I placed in a separate family, seems to contain certain venational features even more primitive than those of Archescytina; and in my opinion the media of some of the Upper Permian Homoptera is more primitive than that of the Kansas forms. So far as the subcosta is concerned there can be no doubt that the condition represented in Archescytina is by far the most primitive; it is entirely independent of the radius and terminates on the costal margin at a point rather remote from the end of R1a. The simplest condition of R is probably that in Permoscytina and Lithoscytina, where it is very little arched at the base and does not have an abrupt bend basally, as in Permopsylla. In all these Lower Permian forms R1 sends a small branch anteriorly, forming the posterior side of the pterostigma, while the main stem of R1 is continued nearer to the apex of the wing. Rs had already attained an unbranched condition and a late origin from R1; undoubtedly the condition which most nearly approaches that of the original Homopteron wing is present in *Permopsylla anomala,* where Rs arises from R somewhat nearer the base than in the other species. So far as the orgin of the media is concerned, I believe that the structure present in Lithoscytina is the most simple; in this fossil it is entirely independent of R at the base, whereas in all other Permian species it is fused with R for about a quarter of the wing-length. In all the Lower Permian Homoptera the media has three branches, M1, M2, and M3 + 4; but in many genera of the Upper Permian family Scytinopteridae (Stenoscytina, Homaloscytina, Elliptoscarta and some species of Orthosctina) the media has four equal or subequal branches; and in at least one species of Orthoscytina the media has three branches, consisting of M1 + 2, M3, and M4,—the opposite of that present in the Archescytinidae. I therefore believe that in the archetype of the Homoptera the media consisted of four subequal branches.[6] The simplest condition of the proximal part of the cubitus is unquestionably represented in Lithoscytina; in this genus alone, of all the Permian Homoptera known, Cu1 is entirely unattached to M and does not even bend towards it basally. The question of the original number of branches on Cu1 is perhaps not so easily disposed of, however. In all the Lower Permian species, except *Permopsylla anomala* it forms a short distal fork, similar to the *areola postica* in the

[6] Tillyard, however, regards the four-branched media as a specialization in the Homoptera, rather than a primitive trait; this is also true of the three-branched cubitus (1926).

psocids. In *P. anomala*, however, it appears to be three-branched, and in many species of the Upper Permian Orthoscytina and Scytinoptera it is also three-branched. Tillyard (1926) argues that the two-branched condition is the original one and the three-branched state a specialization, and he is probably correct; but of course there is also the possibility that the Kansan forms merely represent a line of descent in which the cubitus was reduced to a two-branched condition from an original three-branched one. Cu2 is unbranched and strongly concave in all the Permian Homoptera, and both 1A and 2A are present and unbranched.

In figure 12 I have drawn a hypothetical wing of a Homopteron, with the combined primitive venational features present in the Per-

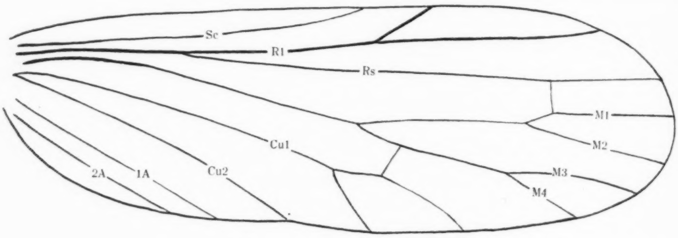

FIGURE 12. Hypothetical fore wing of common ancestor of the Permian Homoptera. For explanation, see text.

mian Homoptera. If our deductions are correct, as I believe they are in all important respects, then this wing gives some idea of the common ancestor of the Homoptera, which must have existed back into the Carboniferous. This hypothetical wing again emphasizes the striking resemblance, already noted by Tillyard and Crampton, between the Palaeozoic Homoptera and Psocoptera. The only outstanding difference between the venation depicted in figure 12 and that of the Permian Dichentomidae is in the structure of Rs, which is forked in the psocids, but unbranched in the Homopteron. When we compare the hind wings of the Permian representatives of these two orders, however, we find great differences. The hind wings of the Lower Permian Homoptera are not known, but in the Upper Permian species they had an expanded anal area similar to that in recent Homoptera. The hind wings of the Permian psocids, on the other hand, were very nearly identical with the fore wings (see figure 13). In

subsequent geological times, of course, the hind wings of the psocids were modified along lines directly opposite those followed by the hind wings of the Homoptera: they were greatly reduced in venation and in size. Since the homonomous condition of the wings in the Permian psocids was apparently a primary one and not a secondary state, and since the venation of the fore wings of the Homoptera was so very close to that of the psocids, it is very probable that the two orders arose from a common ancestor which had homonomous wings, possessing a venation much like that depicted in figure 12, with the addition of a fork on Rs.

Order PSOCOPTERA.

The psocids were taken abundantly in 1932, especially members of the genus Dichentomum. About 150 specimens were found, slightly more than half of which occurred in the upper layer of limestone. But among all these fossils taken in the upper layer, only one belongs to the family Permopsocidae, which apparently indicates that the Permopsocids had greatly decreased in numbers during the interval between the deposition of the two layers of limesone, at least in that vicinity where the rock is now exposed. The new collection of psocids is especially rich in specimens which show the body structure, those from the upper layer revealing many minute details which have not previously been known. A study of this material has added much to our knowledge of Permian psocids, the oldest members of the order known.

Family DICHENTOMIDAE.

Dichentomum tinctum Tillyard.

Figure 13.

Dichentomum tinctum Tillyard, 1926, Amer. Journ. Sci. (5) **11**: 320.
Dichentomum tinctum Carpenter, 1932, ibid., **24**: 7; fig. 1 (complete synomymy given here).

About 125 specimens of this species were collected in 1932. Most of these consist of single fore or hind wings and add nothing to our knowledge of the insect; but there are a few which are more completely preserved than any that I have previously seen. My figure of the fore wing of *tinctum* already published (1932, fig. 1) although correct for the specimen drawn, does not represent the average or commonest form of the wing. In most cases the fore wing is not quite so slender and it has a slight bulge in the anterior margin near the

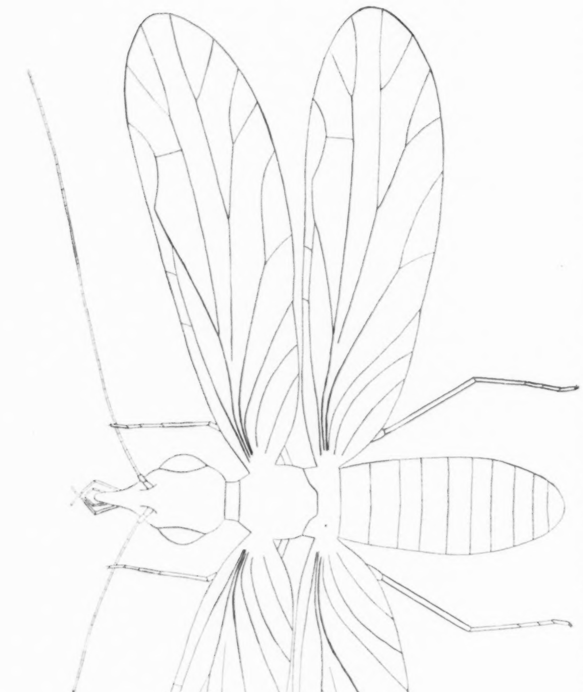

FIGURE 13. Reconstruction of *Dichentomum tinctum* Till. based on several specimens in the Museum of Comparative Zoology.

base. The more typical form of the wing is shown in figure 13. In none of the large number of specimens found is the basal connection of the media visible and I am convinced that this connection had already disappeared by the Lower Permian. In my previous account of these psocids, I stated that the hind wings were essentially the same as the fore wings, not smaller and with a reduced venation as described by Tillyard. This conclusion was based upon several specimens in the 1927 Harvard collection, although as I stated at the time in all of these fossils the hind wings were partially covered by the fore wings. In the new material now at hand there are a few specimens (e. g. No. 3316) which have the fore wings directed forwards and entirely clear of the hind wings. In these we see more distinctly that the fore and hind pairs were alike, the latter being only a little shorter and having a slightly lower areola postica.

The specimens of *tinctum* found in the upper layer furnish us with a nearly complete knowledge of the body structure, as a result of a preservation that is truly remarkable in view of the minute size of the insects. Tillyard (1926, p. 327) has given a restoration of the lateral view of this insect, based upon the type of *Ps. kansasense* (No. 5077, Peabody Museum), and has also presented a more detailed figure of the thoracic and abdominal structure, based upon the type of *Ps. robustum* (No. 5074, Peabody Museum).[7] The latter specimen I examined carefully at the Peabody Museum but was unable to distinguish some of the details which he shows in his figure, such as the small eye situated at the top of the head. The former specimen I was not able to locate in the Yale collection when my previous paper was being written, and I consequently accepted Tillyard's statements concerning the structural features which he described, such as the 5-segmented tarsi and the size and position of the eyes. On a very recent visit to the Peabody Museum I was able to examine this fossil and found that the head and tarsal structure was not nearly so distinct as I had expected. In the new material secured in 1932, however, there are many well preserved specimens which show these structures clearly and also differently from the way in which they

[7] Tillyard figures (1926, p. 325) certain structures which he supposed to be terminal abdominal appendages in this species (based on the type of *Ps. abnormale*, No. 5073, Peabody Museum), but I have already given reasons (1932, p. 2) for regarding these as something entirely foreign to the psocid in question. In none of the new specimens have any such appendages been found.

were depicted by Tillyard. The eyes are obviously very large, and the fore tarsi, at least, are only 4-segmented. These particular specimens in the Harvard collection are so well preserved and the fossils in the Yale collection on which Tillyard based his description so indistinct that I believe there is no doubt of the true condition of these parts in the species under discussion. To show how clearly these portions are preserved in the new fossils, I have included here a photograph showing the head and fore legs as preserved in specimens No. 3324 and 3348 (plate 1). The former specimen is a dorsal view, with the eyes and the palpi splendidly preserved; the latter is a lateral view, the fore legs outstretched and parallel, the tarsi being very distinct. Other specimens show various portions of the body, the following being the most important: No. 3321ab, showing the head, abdomen, and antennae; 3323ab, with clearly preserved legs and abdomen; 3331ab, a fine complete insect, with distinct antennae and fore legs; 3346ab, with excellent antennae; 3347ab, with all legs; 3349ab, the whole insect in lateral aspect; 3353, showing the antennae; 3354ab, with the tarsi (fore?) preserved; and 3357ab, with the antennae.

After a study of these specimens and others not so important, I have prepared a reconstruction of a whole specimen of *Dichentomum tinctum*, by combining these various structures into one individual. The several parts of the insect have been drawn to the same scale by careful micrometric measurements and I believe that the resulting figure gives an accurate idea of the appearance of this insect (figure 13).

There are several features of unusual interest in this insect to which I wish to call particular attention. The head is rather large in proportion to the rest of the body, approaching in this respect the condition in recent psocids. The eyes are also large and prominent, as in the existing members of the order. The antennae are inserted just before the eyes, their insertions being most clearly indicated in specimen No. 3348ab. The first (and possible the second) antennal segment is rather stout and short, but the remaining segments are smaller. The antennae are long and filamentous, being very thin distally, and consist of about 50 segments.[8] The most remarkable feature of the head structure is the presence of what appears to be a

[8] In my previous paper I described the antennae as consisting of about 27 segments. This description was based upon one antenna of a single specimen; in the new material there are several specimens with much longer antennae, which appears to indicate that in the earlier specimen the antennae were broken off near the middle.

short rostrum. This is preserved in so many specimens (see Plate 1) that there can be no doubt of its existence. Such a structure is unknown in other psocids. That this rostrum is not formed by long mandibles shut together is demonstrated by the fact that in a dorsal or ventral view of the insect there is no line of separation visible along the middle. The maxillary palpi are long and apparently three-segmented; the labial palpi are smaller and the segments have not been distinguished. The details of the thorax are still more or less incompletely known; in all specimens the thorax as a whole has the appearance of being crushed or flattened, so that the divisions between the segments are obscure. The length and width of the thorax is easily estimated, but the shape of the different segments has not been ascertained with certainty. I believe, however, that the prothorax is short and more or less in the form of a collar; the mesothoracic segment is clearly the widest and largest, and it appears to have a broad posterior prolongation; the metathorax is rather short and not markedly separated from the abdomen. As for the attachment of the wings, some fossils (e. g. No. 3324) show that the hind wings are attached to the thorax rather far back, as in most recent psocids. At any rate, the hind wings are so broad at the base that they would naturally be placed as far as possible from the fore wings in order to prevent overlapping. The abdomen is well preserved in many specimens; it is rather short, being only about as long as the head and thorax combined, but it is quite similar to that of recent psocids in that respect. Ten segments are visible. I can find no traces of cerci or genital appendages. Certain species show in ventral view a large subcircular disc at the very apex of the abdomen which may be the female genitalia, but no definite structure can be distinguished. As to the legs, I have not seen any specimen which shows the coxae distinctly, this being due to the crushing of the thorax previously mentioned. The femur is slender, and the tibia and tarsus even more so; no tibial spurs are discernible, but they may have been present. I have been able to see the tarsal segmentation with absolute clearness in the fore legs only. The tarsus is long, the metatarsus being about twice as long as the other segments; a pair of small but sharply curved claws is present. The middle tarsus is preserved in some of the fossils, but the segmentation cannot be made out satisfactorily. The hind tarsus is not known to me at all, since the hind legs are usually folded up under the abdomen. In all probability the middle and hind tarsi were similar to the front ones, and I have so drawn them in my figure.

The habitus of *D. tinctum*, as represented in this reconstruction contains many resemblances to that of the recent psocids,—the large eyes and head, short abdomen and particularly the wing venation; but at the same time the homonomous nature of the wings gives an appearance of generalization foreign to the existing Psocoptera.

Dichentomum grande, new species.

Figure 14.

Length of wing: 6 mm.; width, 2 mm.; wing broad, the anterior margin convex, and the inner margin of anal area abruptly curved; costal space broad basally, the anterior margin without the bulge usually present in *tinctum;* Sc giving rise to three veinlets leading to

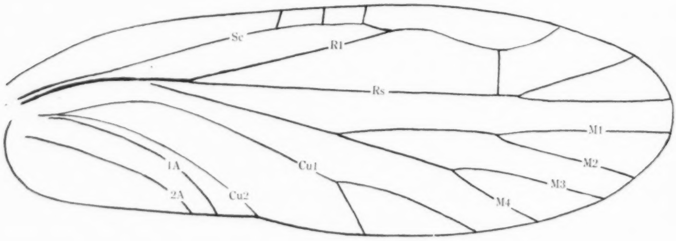

FIGURE 14. *Dichentomum grande*, n. sp., fore wing; holotype, No. 3358ab, Mus. Comp. Zoology.

the margin (this number may be variable); R1 abruptly diverging anteriorly at the origin of Rs; pterostigma very faint; M dividing near the middle of the wing; fork M1 + 2 deeper than fork M3 + 4; Cu1 remote from M at the base, but arched towards it near the origin of Rs, then curved towards the posterior margin; areola postica about twice as long as high; Cu2 smoothly curved, remote from Cu1; 1A close to Cu2 and nearly papallel to it, slightly divergent distally; 2A remote from 1A, not strongly arched.

Holotype: No. 3358ab, Museum of Comparative Zoology; collected by the writer in the upper layer of limestone at Elmo, 1932. The shape of the areola postica indicates that this is probably a fore wing.

This is the largest psocid which has been found thus far in the Elmo limestone. In addition to its size, it is distinguished from the other species of Dichentomum by the strongly arched anterior margin, es-

pecially the basal portion, by the remoteness of Cu1 from M at the base, and by the abrupt bend of the inner margin of the wing. The type specimen is finally preserved, the veins being dark brown and the membrane light brown. Several other psocid wings with similar habitus were also collected in the upper layer, but since the venation is not very clear in any of these, they can be placed here only with some uncertainty.

Family PERMOPSOCIDAE.

Progonopsocus permianus Tillyard.

Progonopsocus permianus Till., 1926, Amer. Journ. Sci. (5) **11:** 338; fig. 14.

Progonopsocus permianus Carp., 1932, ibid., **24:** 12; fig. 5.

Four specimens of this species were collected in 1932, one (No. 3361ab) being found in the upper layer. Only one of the fossils is worthy of note: No. 3363ab. This consists of an excellent fore wing, in which Rs has three branches, the extra branch being on R4 + 5. In all other respects the wing is identical with that illustrated in my figure (1932, fig. 5).

Permopsocus latipennis Tillyard.

Permopsocus latipennis Till., 1926 Amer. Journ. Sci., (5) **11:** 340; fig. 15.

Permopsocus latipennis Carp., 1932, ibid., **24:** 13; fig. 6. (Complete synonymy given here.)

Two specimens of this species were collected in 1932. One, taken in the upper layer (No. 3359ab), consists of three wings and parts of the body. The abdomen and thorax are similar in habitus to those of Dichentomum. The head as a whole is not clear, but the two antennae are preserved. They are about the same in size as represented in my earlier paper, so in all probability the antennae which I described there were complete. They are much shorter than those of Dichentomum.

Lithopsocidium permianum Carpenter.

Figure 15.

Lithopsocidium permianum Carp., 1932, Amer. Journ. Sci. (5) **24:** 15, fig. 7.

One well preserved specimen (No. 3365ab) of this insect was taken in the upper layer, consisting of a single wing, 3.9 mm. long. It has

the same texture as the type, the membrane being heavy in appearance. All veins, including M3 + 4 are much clearer than in the type and several features not visible in the latter specimen are discernible. There is a series of five long and heavy cross-veins between Sc and the costal margin; this is a characteristic not previously found in the Permian psocids and probably represents an ancestral condition in which the subcostal veinlets were even more numerous. The base of Cu1 is more remote from M than I supposed it to be in my description of the type specimen. In my figure of the latter I showed the indentation of the hind margin at the end of 1A; the new specimen demonstrates that this is incorrect, the apparent indentation in the type being due to an inperfection in the preservation. The indentation really is situated at the end of Cu2, as in other psocids. In figure 15 I have redrawn the wing with the addition of the several structures not previously given and with the above correction made.[9]

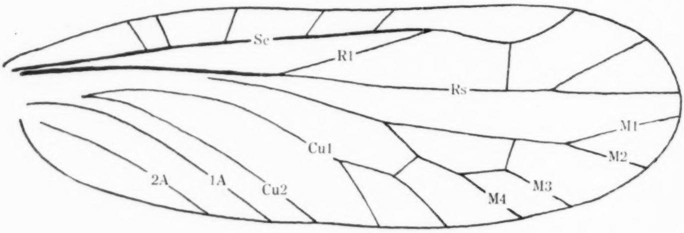

FIGURE 15. *Lithopsocidium permianum* Carp., fore wing, drawn from specimen No. 3365ab, Mus. Comp. Zoology.

Family DELOPTERIDAE.

Among the insects which Dr. Sellards collected in the Elmo limestone thirty years ago there were three closely related species for which he erected the genus Delopterum and the family Delopteridae, and which he placed in the order Protorthoptera. These insects were represented only by fore wings, aside from one or two obscure and twisted portions of hind wings. In the Yale collection from this

[9] This concludes the description of the new (1932) fossils belonging to groups which have previously been treated by the writer in the account of the Sellards and 1927 Harvard collections. The following pages deal with the insects contained in all three collections.

formation Tillyard found twenty-nine specimens of the family, including two species which he described as new. From this material he was able to demonstrate that the hind wings were nearly similar to the fore wings and did not possess the expanded anal area characteristic of the Protorthoptera. A careful study of the venation also led Tillyard to the conclusion that the Delopteridae were most closely related to the Psocoptera (Copeognatha) and he established for them the suborder Embiopsocida. About the same time Martynov published an account of some allied fossils from the Permian of Russia, and after proposing a widely different interpretation of the venation, he designated them as typical representatives of a new order, Miomoptera. In the present paper I shall first describe the new fossils from the Kansas Permian and then discuss the evidence for and against the two views which have been advocated.

In the Harvard collection of insects from the Elmo limestone there are fifty-five more specimens of this family, some of these showing the body structure, which has not previously been known.[10] These fossils enable us to form a more exact picture of the members of this group than has previously been possible, and to correct some erroneous ideas of the classification.

All the Kansan species of Delopteridae are very closely related and agree in the number and arrangement of the main veins.[10] In the case of the cubitus, however, this uniformity of structure has not previously been recognized. Sellards described Cu1 of *minumtum* as "apparently simple," although it was forked distally in his other two species, *latum* and *elongatum*. Tillyard found one specimen (No. 5385)[11]

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[10] Except in the genus Permembia, which, for reasons that will be presented later, I do not consider a member of the family Delopteridae.

[11] Tillyard has designated this specimen as a *paratype* of *minutum* Sellards, but in so doing he has employed that term in a very unusual manner. According to all usage that I have ever encountered, a paratype must be a member of the original series of specimens in the possession of the author of the species when the description is made. In the above instance the specimen designated by Tillyard as a paratype was not even collected until fifteen years after Sellards published his description of the species! This is true of all those specimens in the Yale collection which Tillyard has designated as paratypes of the following of Sellards' species: Psocoptera, *Delopterum minutum*, *D. elongatum*, *D. latum;* Protodonata, *Typus permianus;* Protoperlaria, *Artinska clara*, *A. ovata*, *Paraprisca frigilis*, and *Lecorium elongatum*. I feel that it is necessary to call attention to this peculiar use of the term paratype in order to avoid confusion on the part of future workers, who, not knowing the history of the collections, would naturally assume that all specimens designated paratypes of Sellards' species were part of his collection and were seen by him.

of a fore wing of *minutum* in the Yale collection and he figured and described it also as having an unbranched Cu1. In the Harvard collection there are twenty-six specimens identical with *minutum*, except that Cu1 possesses the distal fork present in all the other Delopteridae. When I examined the Yale fossil figured by Tillyard, I was able to see clearly this same fork of Cu1, as shown in the photograph on Plate 1, figure 4. The Yale specimen is therefore identical with the twenty-six in the Harvard collection, and I believe that we are justified in interpreting Sellards' phrase "apparently simple" as indicating that he was not certain of the structure of Cu1. It seems clear then that the Sellards type, the Yale specimen, and the Harvard fossils belong to the same species, which possessed a forked Cu1.

The specimen in the Yale collection (No. 3394) which Tillyard described as a new species (*dunbari*) is also *minutum*, as I shall show later. Now unfortunately Tillyard, believing that *minutum* possessed an unbranched Cu1, restricted the genus Delopterum to that species and *dunbari* and erected the genus Delopsocus for the other Delopteridae, in which he recognized the presence of a forked Cu1. As we have seen above, however, *Delopterum minutum* really possessed a similar Cu1, so that the distinction between these genera does not exist, making Delopsocus identical with Delopterum.[12]

With these modifications, and exclusive of the genus Permembia, the Lower Permian Delopteridae include a series of small insects, having a wing expanse of ten or fifteen millimeters; the body was short, the wings extending far beyond the abdomen at rest; the antennae were prominent and rather stout, with 12 or perhaps 13 segments, each about twice as long as broad; the tarsi were 4-segmented, and terminated in a pair of prominent claws. In the fore wing, R1 was feebly forked distally in the region of the weak pterostigma; Rs included three branches, R2, R3, and R4 + 5; M was fused with Cu1 for some distance proximally and possessed two long branches (M1 + 2, M3 + 4); Cu1 was forked to form a distinct areola postica; Cu2 and the two anal veins were unbranched. The hind wing was similar to the fore except that M was fused with Cu1 at the very base of the wing only; and that Cu2 was coalesced for its entire length with Cu1, the compound vein appearing as a concave vein, in place of a convex Cu1, as in the fore wing. The areola postica of the hind wing was a

[12] If the genus Delopsocus Tillyard (1928) is the same as Pseudomantis Martynov (1927), as Martynov contends (1930), then Pseudomantis now becomes synonymous with Delopterum Sellards (1907).

little higher and shorter than that of the fore wing. Cross-veins were few in both pairs of wings, but the humeral cross-vein (hm) was always distinctly formed.

Genus *Delopterum* Sellards.

Delopterum Sellards, 1909, Amer. Journ. Sci., (4) **27**: 168.
Pseudomantis Martynov, 1927, Zool. Anz., **52**: 105.
Delopterum Tillyard, 1928, Amer. Journ. Sci. (5) **16**: 471.
Delopsocus Tillyard, ibid., p. 474.

Fore wings: Sc usually ending before the middle of the wing and connected by a distal cross-vein to R1; Rs arising at about one-fourth the wing length from the base; R4 + 5 originating near the middle of the wing; M separating from Cu1 just before the origin of Rs; M1 + 2 and M3 + 4 diverging at the middle of the wing. Hind wing: similar to the fore wing, with the exceptions noted for the family.

Genotype: *Delopterum minutum* Sellards.

Delopterum minutum Sellards.

Figure 16; plate 1, fig. 4.

Delopterum minutum Sell., 1909, Amer. Journ. Sci. (4) **27**: 168; fig. 16.
Delopterum minutum Tillyard, 1928, ibid. (5) **16**: 472; fig. 1.
Delopterum dunbari Tillyard, 1928, ibid., p. 473; fig. 2, 3.

Fore wing: length, 4.3–4.6 mm.; width, 1.4, mm.; Sc usually terminating at about one-third the wing length from the base; R2 + 3 joined to R1 by an oblique cross-vein; M1 + 2 and M3 + 4 separating below the origin of R4 + 5; areola postica usually about twice as long as high. Hind wing: length, 4.3; width, 1.8 mm. Anterior margin slightly concave basally; Rs directed away from R1 at the very base; cross-vein between R2 + 3 and R1 as in fore wing; areola postica about as high as long; 1A and 2A straight, slightly diverging distally. Length of body, 3.4 mm.; thorax, 1.2 mm.; abdomen, 1.6 mm. The holotype of this species was No. 64 in the Sellards collection, but unfortunately that specimen has been lost. As the neotype of the species I designate specimen No. 3295ab, in the Museum of Comparative Zoology; this consists of all four wings and the body, showing the head, thorax, and abdomen. It was collected by the writer in the upper layer of limestone in 1932.

I have already shown above that Cu1 of this species is forked as in

other members of the family and I believe that there is no doubt that *dunbari* is identical with *minutum*. The distinctions on which Tillyard based this species, such as the apparent absence of cross-veins, depend entirely on preservation. The main characteristic which he emphasized, the double forking of Cu1, does not exist; Cu1 has only the normal areola postica, shaped as in *minutum*. The hind wing of this species is also not quite as depicted by Tillyard; the fossil on which he based his figure lacked the posterior margin proximal of the

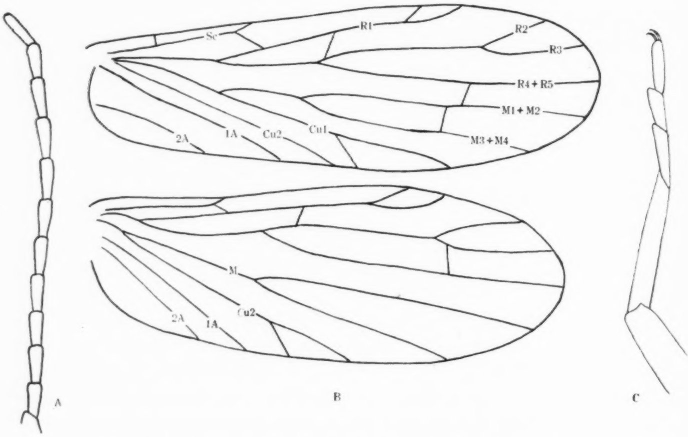

FIGURE 16. *Delopterum minutum* Sell. A, antenna, drawn from specimen No. 3209ab; B, fore and hind wings, based on specimens No. 3203ab; C, hind (or middle) tarsus. drawn from specimen No. 3201ab.

termination of M. The wing is really a little broader than the fore, with a more prominent anal area, although the latter is not expanded. The cross-veins of both wings are usually only faintly preserved and are frequently indicated merely by slight bends in the longitudinal veins which they connect. Certain of the cross-veins, such as the subcostal cross-vein and the one between R2 + 3 and R1, are always distinctly preserved and were undoubtedly more strongly developed than the others. In the Harvard collection there are twenty-six specimens of *minutum*, collected by the writer in the Elmo limestone during 1927 and 1932; only two of these (No. 3295ab and 3304ab)

were found in the upper layer. Specimens No. 3203ab is an excellent fore wing, the cross-veins and origins of the main veins clearly indicated. No. 3204ab, 3205ab, 3206ab, 3207ab, 3299ab and 3303ab are complete fore wings, well preserved. No. 3202ab, 3298ab, 3301ab, and 3302ab are good hind wings, although Sc is faintly preserved in the first of these. No. 3208 shows a hind wing and parts of the body; No. 3209ab includes the hind wings and parts of the body, even the antennae; No. 3200ab shows parts of all wings and body, including portions of the antennae; No. 3295ab shows the four wings and body, without the antennae. No. 3201ab is a lateral view of the whole insect; most of the fore and hind wings were originally showing, but parts of these were later removed in order to reveal the body structure; the bases of both antennae and one whole antenna are preserved, although the segmentation is not so clear as in specimen No. 3209ab; the tarsus of a fore leg and a tibia and tarsus of a hind (possibly middle) leg are also present. The latter is particularly well preserved, showing four distinct tarsal segments and the apical claws. The metatarsus is more than twice as long as the others, but the outlines of the other segments are so distinct I do not believe that there is any possibility that this basal segment really consists of two separate segments.

Delopterum elongatum Sellards.

Delopterum elongatum Sellards, 1909, Amer. Journ. Sci. (4) **27:** 168; fig. 20.

Delopsocus elongatus Tillyard, 1928, ibid. (5) **16:** 475; fig. 4, 5.

Delopsocus fasciatus Tillyard, 1928, ibid. p. 476; fig. 6, 7.

Fore wing: length, 5.5–6.5 mm.; width, 1.8–2 mm. Sc usually terminating at about the middle of the wing; M dividing almost below the origin of R4 + 5; areola postica shaped as in *minutum*. Hind wing: length, 5.8 mm.; width, 1.8 mm. The oblique cross-vein between R1 and R2 + 3 is absent.

The holotype of this species was No. 61 in the Sellards collection, but that having been lost, I designate specimen No. 3210ab in the Museum of Comparative Zoology as the neotype. A photograph of Sellards' type, which I made in 1927, is in the Museum of Comparative Zoology.

This species is very similar to the preceding one, but it is larger. The only venational differences are the longer subcosta and the fewer cross-veins. The anterior margin of the fore wing is nearly straight,

as in *minutum;* this is true of the specimen in the Yale collection, which Tillyard has figured as having a distinctly convex anterior margin. The venation of the hind wing is like that of *minutum*, Cu and M originating as in that species, not as represented by Tillyard in his figure.

D. fasciatum Till., which was based upon the presence of a brown color pattern, is unquestionably synonymous with *elongatum*, in my opinion. Indications of the color pattern in various degrees of intensity can be seen in several specimens of *elongatum*.[13] Tillyard's figures indicate that the areola postica in *fasciatum* is quite differently shaped from that of *elongatum*, but the figure of the latter is incorrect in this respect.

In the Harvard collection there are five specimens of *elongatum*, of which only one (No. 3305) is from the upper layer of limestone: No. 3210ab, 3305, 3306ab, 3307ab, fore wings; No. 3212, a hind wing, with the very base missing. Specimen No. 3211ab, a fore wing, may also belong here, but it is rather small (length, 5.2 mm.).

Delopterum latum Sellards.

Delopterum latum Sellards, 1909, Amer. Journ. Sci. (4) **27**: 169; fig. 17.
Delopsocus latus Tillyard, 1928, Amer. Journ. Sci. (5) **16**: 475; fig. 8, 9.

Fore wing: length, 6 mm.; width, 1.9 mm.; Sc usually terminating before the middle of the wing; M dividing proximad of the origin of $R4 + 5$; areola postica a little higher than in the two preceding species; anal area broad; 2A sigmoidally curved and possessing a short posterior veinlet (possibly a cross-vein). Hind wing: length, 5 mm.; width, 1.7 mm.; venation apparently as in other species. I am unable to discern the diverging branches of 2A in the hind wing which Tillyard figured.

The holotype of this species was originally No. 94 in the Sellards collection, but since that has been lost, I designate as the neotype specimen No. 3214ab (lower layer of limestone) in the Museum of Comparative Zoology. This species is easily recognized by the broad fore wing. In other respects the wing is shaped like those of *minutum* and *elongatum*, the convexity of the hind margin of the specimen

[13] That the presence or absence of the color pattern in fossil insects from the Elmo limestone may be a matter of preservation is shown most clearly in the case of the Palaeodictyopteron *Dunbaria fascipennis*, some specimens of which show a very definite color scheme, while others possess only the faintest traces of coloration.

figured by Tillyard being due to a deep depression in the matrix at this point. The cross-vein leading from 2A is a distinctive feature not found in the other species.

In the Harvard collection there are five specimens of *latum*, all from the lower layer: No. 3214ab, a complete fore wing, showing the humeral cross-vein; No. 3213ab, 3215, and 3308ab, complete fore wings, No. 3215 showing the cross-vein between M3 + 4 and Cu1a very clearly; No. 3216ab, a good hind wing, showing the costal space narrowed basally. Three other specimens, No. 3309ab, 3218ab, and 3217, probably belong here also, but they are not well preserved.

The Relationships of the Delopteridae.

In addition to the Kansan species above, insects belonging to the family Delopteridae have been found in the Upper Permian of Russia. As far back as 1904 Handlirsch described a fore wing of an insect from these beds under the name of *Palaeomantis schmidti,* and he also gave a description of a badly preserved hind wing, with an expanded anal area, which he considered to be the hind wing of the same species. From a study of these fossils he came to the conclusion that they belonged in the Orthopteroid series, related to the Mantids, and he erected for them the family Palaeomantidae. In 1927 and 1928, nearly a year previous to the publication of Tillyard's account of the Kansan Delopteridae, Martynov described two related genera from the Permian of Russia, Pseudomantis and Miomatoneura, placing them, together with Delopterum in a new order, Miomoptera. In a later paper (1930) he published a more complete account of the Palaeomantidae, which he regards as typical of the order Miomoptera.

Some confusion of names has been introduced into the literature pertaining to these insects, partly because Tillyard did not see Martynov's 1927 paper before the publication of his work on the Kansan Delopteridae:

1. Martynov contends that the family Delopteridae is identical with the Palaeomantidae, the latter name having priority. This, of course, would be the case if Palaeomantis and Delopterum belonged to the same family; but I do not believe this is supported by the facts. The venation of the fore wing of Palaeomantis is decidedly different from that of Delopterum, even as represented in the revised figure published by Martynov (1930; pl. 13, fig. 1). a) In this genus there is a series of veinlets between Sc and the front margin of the wing and also between R1 and Sc in the basal half of the wing; these veinlets

are absent in Delopterum. b) Cu1 in Palaeomantis has three well developed branches, but in Delopterum it has only two. c) 1A and 2A arise as distal branches of a common vein in Palaeomantis, but do not do so in Delopterum. These features seem to me to be sufficient to require the separation of Palaeomantis and Delopterum into distinct families. Martynov has described and figured (1932) a fossil which he considered to be the hind wing of *Palaeomantis schmidti*, but he made this determination simply because the hind wing in question was approximately the same as in Delopterum. It differs distinctly from the fossil which Handlirsch supposed to be the hind wing. I therefore believe that Palaeomantis and Delopterum belong to different families, Palaeomantidae and Delopteridae.

2. Martynov also claims that the genus Pseudomantis (1928) and Delopsocus Tillyard (1928) are identical and in this I believe he is correct. The fore and hind wings of the specimens of Pseudomantis are so similar to those of Delopsocus that if they had been found in the same beds they would probably been placed in the same species. But as I have already shown above, Delopsocus Tillyard is really identical with Delopterum Sellards (1907), the venation of the latter having been misunderstood by Tillyard. Consequently, Pseudomantis Martynov is synonymous with Delopterum Sellards.

To recapitulate then, the family Delopteridae, as defined above, consists of two genera:

Delopterum Sellards (1907) (= Pseudomatis Mart., Leptoneurula Mart.,[14] Delopsocus Till.), known from the Lower Permian of Kansas and the Upper Permian of Russia.

Miomatoneura Martynov (1927), from the Upper Permian of Russia.

As already stated Tillyard concluded that the Delopteridae were most closely related to the Psocoptera and he established for them the suborder Embiopsocida. Martynov, on the other hand, was led to the belief that they were not related to the psocids but to the Lemmatophoridae of Sellards. The latter were previously designated by Tillyard as typical members of the new order Protoperlaria, allied to the Perlaria. Martynov, however, regards the Lemmatophoridae, together with the Delopteridae, Probnisidae, and certain other Permian families, as constituting the order Miomoptera, with very different affinities. Martynov's conclusions were based upon the following points:

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[14] Leptoneurula Martynov (1928) was synonymized with Pseudomantis by Martynov himself (1930).

1. The coalescence of M and Cu1 is present in the fore wing of the Delopteridae and is frequently found in the Lemmatophoridae, but is not known in the psocids.

2. The wing surface of the Delopteridae and Lemmatophoridae is covered with hairs, whereas that of the Permopsocida is devoid of hairs. In this connection it should be borne in mind that Tillyard was mistaken in his belief that the wing surface of the Delopteridae was the same as that of the Dichentomidae and Permopsocidae (Permopsocida). The hairs are plainly visible in many specimens of Delopterum.

3. Rs originates more distally in the hind wing than in the fore wing in the Delopteridae and the Lemmatophoridae, but not in the psocids.

4. M is fused with Cu for a shorter distance in the hind wing than in the fore wing of the Delopteridae and Lemmatophoridae, which is not true of the psocids.

5. In *Delopterum latum* 2A divides into two branches as in the Lemmatophoridae, but this is not found in the psocids.

6. CuP (Cu2) is lacking in the hind wing of the Delopteridae and also, according to Martynov's interpretation, of the Perlaria and Embiaria, but not in the hind wing of the psocids.

7. The reduced anal area of the Delopteridae, which seems at first glance to separate these insects from the Lemmatophoridae and their allies (Perlaria) may have been secondarily acquired, as in the case of some Recent perlids, as Chloroperla.

8. In both fore and hind wings of the Delopteridae MA is fused with Rs basally and arises from Rs as a branch of that vein near the middle of the wing. This coalescence of Rs and Ma occurs commonly in some species of Lemmatophora, but is unknown in the psocids.

Now at the time when Martynov's paper was written, his knowledge of the hind wing of the Permian psocids was based upon Tillyard's description, which was far from correct, however. As a consequence the 3rd and 4th arguments listed above lose their weight. The 5th argument is also without significance for the anal vein in *Delopterum latum* which Martynov supposed to be 2A is merely a cross-vein leading to the hind margin; it is at most a specific characteristic and of no phylogenetic value. The 7th argument is of a negative nature only; that is, it merely attempts to explain away an obstacle between the Delopteridae and the Lemmatophoridae, but it does not disprove the possibility of relationship between the Delopteridae and the

psocids. As to the 2nd argument, the trichiation of the wings, although it is true that the Permian psocids, Dichentomidae and Permopsocidae, had no hairs on the wings, many species of Recent psocids, especially of the family Amphientomidae, have both scales and hairs on the wing membrane. Obviously then the presence of hairs in the Delopteridae has no weight in eliminating them from the psocids. Finally, in considering the 8th argument, we must bear in mind that there is no evidence whatever that MA has fused with Rs in the Delopteridae, as Martynov contends. There is no indication of the divergence of MA from MP at the base of the wing. It seems to me that the only reason why Martynov supposed this fusion to have taken place in the Delopterids, was because it has done so in the Lemmatophoridae. This argument is therefore worthless, depending upon the assumption of the conclusion to be proved.

Apparently, then, from this series of arguments against the idea that the Delopteridae are members of the Psocoptera, only two have any significance, the 1st and the 6th. These alone are hardly sufficient to disprove such a relationship. Furthermore, it is not difficult to find characteristics of equal or even greater significance which differ in the Delopteridae and the Lemmatophoridae. In the latter, for example, Cu1 (or CuA of Martynov's nomenclature) is obviously 3-branched, the first branch arising so close to the base of the wing that it appears to be an independent vein. This condition is entirely opposite to that in the Delopteridae. And regardless of Martynov's attempt to explain away the difference in the structure of the anal area of the hind wing of the Delopteridae and the Lemmatophoridae, I believe that this is still the main objection to the thesis that these two groups of insects are closely related. In the Delopteridae the veins in the anal area of the fore wing are the same as those in the anal area of the hind wing, there being only the two unbranched veins 1A and 2A. In the Lemmatophoridae as well as all other Protoperlaria and nearly all Perlaria, the anal area of the hind wing is much expanded and contains numerous branches of the anal veins which are absent in the fore wing and which were apparently developed to support the extra membrane. Now if such an enlarged anal area were reduced to a small one, as Martynov contends to have been the process which produced the small anal area of the hind wing in the Delopteridae, then we should expect to find in the reduced wing some traces of the extra branches of the anal veins. Such is the case, for example, in the perlid Nemoura, which Martynov cites as an ex-

ample of this reduction. But as I have already stated, in the Delopteridae the anal veins are unbranched and similar in both pairs of wings.

The body structure of the Delopteridae is much more like that of the Psocids than like that of the Lemmatophoridae. The new fossils described in this paper show that cerci were absent in the Delopteridae and in the Permian Psocoptera, although they were well developed in the Protoperlaria. In both the Delopteridae and the Permopsocida the abdomen was short and the tarsi were 4-segmented; whereas in the Protoperlaria the abdomen was long and the tarsi were 3-segmented.

In closing this account of the Delopteridae, I therefore believe that we are justified in concluding that there is more evidence that the Delopteridae were closely related to the Psocoptera than that they were allied to the Lemmatophoridae and the other families which Martynov included in the order Miomoptera. I am still inclined to accept Tillyard's view that the Delopteridae were an aberrant branch of the Psocids which died out without giving rise to any other group of insects known to us at the present time. Perhaps the unusual nature of the hind wing, with the complete fusion of Cu1 and Cu2, was the result of a tendency to narrow the hind wing, for such a line of descent was obviously followed by the Psocoptera which have persisted through the geological ages and up to the present era. The thorax of the Delopteridae as well as that of the Permopsocida was hardly large enough to bear two homonomous wings which the Dichentomidae and Permopsocidae possessed. Even in the Recent psocids, in which the hind wings are much reduced, they are attached far back on the thorax, in many families seeming to arise from the abdomen. It is not unreasonable to assume that the Delopteridae represent one line of descent of the Psocoptera in which the hind wing had already begun to be narrowed in a unique method, but which was not able to persist for as long a time as some other lines of development.

Order PROTELYTROPTERA.

Probably the most remarkable insects of the entire fauna of the Elmo limestone are the elytrophorous species to which Tillyard has applied the ordinal name Protelytroptera.[15] These fossils, although

[15] In his paper on these fossils (1931) Tillyard used the term Elytroptera as well as Protelytroptera in reference to the order. Although the former would perhaps have been more suitable, the latter is the one which he employed first, in the definition of the order, and therefore has priority.

not common in the limestone, are by no means as rare as some other groups. In the Yale collection Tillyard found seventeen specimens; in the Sellards collection I have identified one specimen and in the Harvard material fifty-six specimens belonging to this order. Most of these fossils consist of a single elytron, which resembles closely a coleopterous elytron with a feeble venation; but a few specimens have been found which show the structure of the hind wings and certain portions of the body.

Through the courtesy of Professor Dunbar, I have been able to examine the Yale specimens in the Peabody Museum, which were studied by Tillyard. From my examination of the entire series of seventy-four specimens, I believe that it is necessary to revise somewhat Tillyard's classification of these insects and to modify certain of his statements regarding the wing and body structure. These changes are only to be expected, of course, inasmuch as I have worked on more than four times as many specimens as were seen by him.

Although there are some structural features, such as the mouthparts, on which we are entirely uninformed, we do know the general habitus and a few details of the body. The head was small but broad; the eyes prominent, convex, situated well back on the sides of the head; the antennae, in Protelytron at least, were rather short and thick, consisting of about twenty-two loosely jointed segments; the pronotum was longer and wider than the head and shaped like an oval disc, closely resembling that of some Carboniferous Protorthopteroids. The fore legs are not known, but the middle and hind legs possessed five tarsal segments, the fifth being the longest; the hind legs in both Protelytron and Acosmelytron were robust and had very short tarsal segments; the distal part of the tibiae bore a series of spines and teeth, which were probably used to assist in the folding of the hind wings, as is the case with many beetles. The middle legs in Parablattelytron and probably all other members of the order were more normal and slender, with the last tarsal segment the longest. The abdomen was a little shorter than the elytra and was covered by them at rest. The fore wings were typical elytra, strongly convex, with a prominently widened costal area (ce) at the very base, which was not observed by Tillyard in the Yale fossils. In the more generalized forms Sc, R1, Rs, Cu1, Cu2 and three anal veins were present, and there was also a submarginal thickening nearly paralled to the posterior border, forming the sutural margin (sm); in the more highly modified species only the bases of R1, Sc, and Cu2 are discernible.

All the veins in the elytra were convex, including the subcosta, except Cu2. At the base of the wing the subcosta is margined anteriorly by a deep furrow, which resembles and may be homologous to the epipleural fold of the coleopterous elytra. The hind wings were much enlarged, with an expanded and folded anal area, though the usual longitudinal veins were reduced and confined to the anterior part of the wing.

As far as the structure of the wings is concerned, there is every indication that the Protelytroptera had already differentiated into several distinct families by the time of the lower Permian. The following families were recognized by Tillyard:

1. Protelytridae, including those species in which the sutural margin is broad and evenly developed along the whole of the posterior border. In this family Tillyard placed two genera, Protelytron and Protelytropsis.

2. Permelytridae, including those species having the sutural margin broad from the base to about half way along the posterior border, then narrow or obsolete for the remaining length of the elytron. Two species and genera were placed here, *Permelytron schucherti* and *Megelytron robustum*. After examing the type of *schucherti* (No. 5411ab, Peabody Museum), I suspected that the distal part of the sutural margin was not actually narrowed as described by Tillyard, but only covered up by a part of the rock in which the elytron was preserved. I therefore used a fine needle on this part of the fossil and found that my suspicions were correct: *the sutural margin was uniformly developed along the entire posterior border,* as in all of the other Protelytroptera in which it is present. With the elimination of this supposed family characteristic the genus Permelytron becomes a member of the Acosmelytridae, as I shall show later. In the type of Megelytron, the elytra are folded back over the abdomen, the posterior portions are broken away, for some distance distad of the middle of the wing (as shown in Tillyard's figure), and the apical part is very obscure. I do not believe that a true sutural margin was present in this insect at all, but at any rate Megelytron differs so markedly from the other Protelytroptera that it certainly requires a distinct family for its reception.

3. Blattelytridae, including the species in which the venation is more or less atrophied and reduced, but always showing the basal part of Cu2 (*vena dividens*). In this family Tillyard placed two genera, Blattelytron and Parablattelytron. It is unfortunate that

the genus Blattelytron, from which the family name is derived, is known only from a single fragment of an elytron lacking the proximal two-thirds of the anterior margin, and the whole base, and being very poorly preserved. From my examination of this specimen I am inclined to believe that a sutural margin was present in this insect. Tillyard states that there is "no clear indication of a sutural margin," but if we bear in mind that the fossil is very poorly preserved and fragmentary, and that poor specimens of Protelytron show no signs of a sutural margin, I think that the explanation of the apparent absence of the sutural margin on the grounds of poor preservation is acceptable. With this assumption, it is clear that Blattelytron and Parablattelytron are members of the same family, as they were regarded by Tillyard. But if Blattelytron should turn out to have lacked a sutural margin, then it would require a distinct family.

4. Acosmelytridae, including those species with an atrophied venation, not even Cu2 being visible. A single genus, Acosmelytron, with three species, was placed here. From my study of the Yale types I am convinced the apparent absence of the basal part of Cu2 is merely the result of poor preservation of these three specimens. In two of these, *acutum* and *elongatum*, I could distinguish the basal part of Cu2 as clearly as the basal parts of R and Sc which Tillyard described; and in the third species, *delicatum*, I was unable to see any veins at all. However, even if we assume that Cu2 in Acosmelytron is less developed than that in Parablattelytron and Blattelytron, I do not consider that difference sufficient to separate these genera from the Blattelytridae.

In my conception, then, the previously described Protelytroptera from the Lower Permian can be grouped into the three families Protelytridae, Megelytridae (new family), and Blattelytridae. But in the new material constituting the Harvard collection there are in addition representatives of two other families, as widely divergent from one another and from the three former families, as the latter are from each other. One of these, Archelytridae, is characterized by having a 3-branched Cu1 in the elytron; the other, Elytroneuridae, is distinguished by having a much narrowed anal area, a remarkably broad costal region, and no sutural margin. I have also found in this material a new genus, Permelytropsis, which is characterized by the absence of Cu2 and which I have placed in the Protelytridae.

The classification used in this paper is given in the following outline:

Family Protelytridae.
- Genus Protelytron Tillyard.
- Genus Protelytropsis Tillyard.
- Genus Permelytropsis, new.

Family Megelytridae.
- Genus Megelytron Tillyard.

Family Blattelytridae.
- Genus Blattelytron Tillyard.
- Genus Permelytron Tillyard.
- Genus Parablattelytron Tillyard.
- Genus Acosmelytron Tillyard.

Archelytridae, new family.
- Genus Archelytron, new.

Elytroneuridae, new family.
- Genus Elytroneura, new.

Family PROTELYTRIDAE.

Elytron: Sc, R1, Rs, M, Cu2, 1A, 2A, and 3A present and unbranched; Cu1 present except in Permelytropsis, new genus; costal area broad; sutural margin well developed.

Genus *Protelytron* Tillyard.

Protelytron Tillyard, 1931, Amer. Journ. Sci., **21**: 239.

Elytron: costal margin convex, the costal expansion (ce) at the base being very prominent; Sc strongly developed at the base, but becoming weak near the middle line of the elytron and apparently disappearing at this point; costal area broad, with patches of short, stout spines, at least near the subcosta; Rs arising at the middle of the wing or beyond; M arising from the base, free from Rs and Cu1; Cu1 and Cu2 unbranched, diverging at the base of the wing; 1A, 2A, and 3A straight and nearly parallel; a fourth anal vein may be present; inner margin of the anal area rounded.

The head is wide, with prominent eyes, and probably small mouthparts; antennae with about 24 loosely jointed segments, the basal one being short and cylindrical; body flattened, the pronotum wider than the head, with rounded margins. The fore and middle legs are unknown in this genus, but the hind legs are stout, the trochanter being spherical; the femur is thick, being only about three times as long as wide; the tibia is narrow basally but wide distally, with several teeth on the outer distal margin; the first four tarsal segments are thick and short,

and each bears at least two spines distally; the last tarsal segment is about twice as long as the others and is more slender; there are two large terminal claws.

Genotype: *Protelytron permianum* Till.

In this genus Tillyard placed two species, *permianum* and *dunbari*. The former was based upon a single finely preserved specimen consisting of one elytron, both hind wings, and portions of the body. *Dunbari* was based upon three specimens: No. 5418ab (Peabody Museum), the holotype, consisting of two elytra, more or less complete, and the distal part of one hind wing; No. 5405ab (paratype), consisting of two elytra lying nearly parallel along the abdomen, and faintly preserved portions of the hind wings; and No. 5417 (paratype), consisting of two elytra folded back over the abdomen, completely concealing the hind wings. I believe that the former paratype (No. 5405) does not belong to the same species as the holotype and the other paratype (No. 5017), and that the species (*dunbari*) represented by the latter fossil is the same as *permianum*. Tillyard separates his two species of Protelytron on the following points of difference:

1. The shape of the apex of the hind wing. Tillyard states that in *dunbari* the apex of the hind wing is widely and bluntly rounded, as shown in his figure 4.[16] On examining the holotype specimen, I came to the conclusion that the real apex of the wing was probably still covered up by the matrix; by chipping away the matrix at this part, I found that this was in fact the case, and that *the apex of the hind wing was in reality shaped exactly like that of permianum.* A comparison of the hind wings of the holotypes of *permianum* and *dunbari* now showed no differences whatever. In the paratype No. 5405ab the venation of the hind wing is very obscure and the apical part is not even preserved. In paratype No. 5017 none of the hind wings are visible.

2. The size and shape of the elytra. Tillyard characterized the elytra of dunbari as being narrower, smaller, and having a narrower

[16] According to the caption under this figure the drawing was based on specimen No. 5405ab (paratype), but I think it more than likely that it was really based on the holotype (No. 5418ab). The venation in the hind wing of the former fossil is very indistinct and is not even preserved in the apical part, which is the portion figured. In the holotype, on the other hand, the apical part of the wing is very clear and the contour of the apex before I cleaned the specimen was exactly as shown in Tillyard's figure. The present discussion, however, does not depend upon the assumption of such an error in labelling the figure.

costal area than those of *permianum*. The elytra of the holotype and paratype No. 5417 of *dunbari* are very similar to each other and so far as I can see similar to those of *permianum*. They are 5.5 mm. long, only .3 mm. less than those of the latter species; the dimensions of the width are not given by Tillyard, but I find them to be about the same as those of *permianum*, so that the elytra are shaped as in the latter insect. I am unable to distinguish any differences in size or shape of the costal field. The other paratype (No. 5404ab), however, has very different elytra; they are much smaller in proportion to the size of the entire insect, so that the abdomen extends beyond them.

3. Minor venational features, such as the indistinct subcosta and a slight difference in the place of termination of R1. The degree of distinctness of the subcosta or any other vein which was originally weakly chitinized is unquestionably dependent upon preservation to a large extent; an examination of a series of protelytropterous elytra shows a variation of the clearness of the veins in proportion to the degree of preservation of the whole elytron. Also the point of termination of R1 and of the other main veins in these elytra seems to be subject to slight variation in various individuals.

For the reasons given above, I consider the holotype and paratype No. 5017 of *dunbari* to be identical with *permianum*, and accordingly regard *dunbari* as a synonym of the latter species. The other paratype, No. 5405ab, apparently belongs to a distinct species, which will be described below as *tillyardi*.

Protelytron permianum Tillyard.

Figures 17, 18 (A, B).

Protelytron permianum Tillyard, 1931, Amer. Journ. Sci., **21**: 240; fig. 1–3; 14, 15.

Elytron: length, 5.3–6 mm.; width, 1.7–2 mm. Costal area very broad; R and R1 nearly straight; Rs usually arising just beyond the middle of the wing; M straight, terminating on the sutural margin near its termination; Cu1 and Cu2 and the anal veins straight; sutural margin wide; the patch of spines on the costal area is large, extending to about the middle of the wing; another cluster of stout spines is located on the basal part of the sutural margin. Hind wing: length, 8 mm.; width, 6 mm. In figure 17 I have shown the complete venation of the hind wing, based mainly on specimen No. 3366ab in the Museum of Comparative Zoology, although the type specimen

No. 1019a in the Peabody Museum was also used to verify certain doubtful points. It will be seen that my figure differs somewhat from that given by Tillyard. This is mainly due to the fact that the hind wings are more clearly preserved in the Harvard fossil than in the specimen which Tillyard studied. Of course the venation of any wing which is adapted for folding, as these hind wings were, is naturally

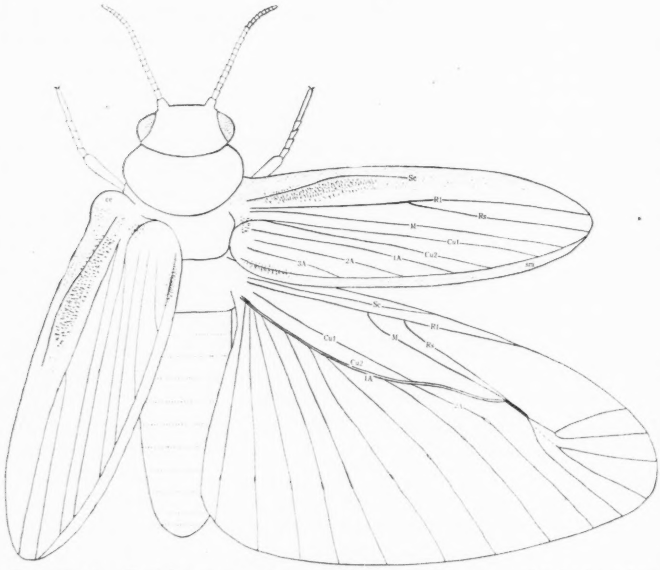

FIGURE 17. *Protelytron permianum* Till. Reconstruction, chiefly based on specimen No. 3266ab in the Museum of Comparative Zoology. For explanation, see text.

more difficult to interpret in the fossil state than the venation of a wing which is normal and has no lines of folding or creasing. The chance or error in working out such a venation obviously decreases in inverse ratio to the number of specimens available for study, and it is therefore only logical to expect that certain corrections will be made as more and more material is accumulated. So far as the anterior part of the wing is concerned, i. e., that section including

the main veins, I believe that we now have a fairly accurate picture of the venation; but I am not certain of the exact number of radiating veins in the anal fan. The principle differences between Tillyard's figure and mine lie in the number of branches leading from R and from the fulcrum; and the identity of M and 1A. In both wings of the Harvard fossil two branches can be seen leading from R1; the more distal of these is presumably Rs, which leads to the fulcrum, passes beyond and forms two branches which bend abruptly upwards; the second vein arising from R is apparently M, which leads to the fulcrum and seems to end there; but just beyond that point there is a distinctly forked vein which I assume to be the end of M, though it may be another branch of Rs. In the area between the origin of Rs and the branches R2 and R3, i. e., directly above the fulcrum, I can discern no veins whatever. In this area Tillyard shows several more or less oblique and uncertain veins, but these are no more than wrinkles or creases in the membrane. In the distal part of the wing Tillyard shows a series of pectinate veins, directed towards the apex; this part is poorly preserved in the Yale specimen but is very clear in the Harvard fossil. It is the one part of the wing about which there can be no doubt as to the nature of the venation. Below M another vein can be distinguished, but this is well down near 1A; it leads from the base of the wing and terminates on 1A just beyond the origin of Rs, well before the fulcrum. This vein is convex and I consider it to be Cu1. Parallel and contiguous with 1A is a concave vein which is probably Cu2. 1A is a strong vein, the strongest in the wing; at first it curves posteriorly but is then directed anteriorly and finally terminates on the fulcrum. Between M and the concave vein which I have called Cu2, Tillyard figures two veins, both arising from a short stem at the base and then coalescing again distally, thus forming a closed lanceolate cell. The anterior of these veins he designated as Cu1 and the lower as Cu2. Tillyard characterized the former of these as "weakly chitinized" and the second as "a deep furrow, barely if at all chitinized." From my examination of the Yale fossil I am inclined to consider that neither of these structures represent true veins but only lines of folds or creases, which are numerous in the specimens and some of which are indicated by dotted lines in Tillyard's figure. In the Harvard fossil I cannot make out the two weakly chitinized veins described by him, whereas the veins which I have indicated as Cu1 is a strongly chitinized structure; since this is a true vein, then there is not space in the same area for the veins

which are depicted by Tillyard. In both the Harvard and Yale fossils a vein can be seen leading from the distal end of the fulcrum and terminating below the apex. This is probably the end of 1A, or at least a branch of that vein. The remaining veins in the hind wing, all of the radiating type, are in all probability composed of 2A, 3A, and perhaps some auxiliary veins.

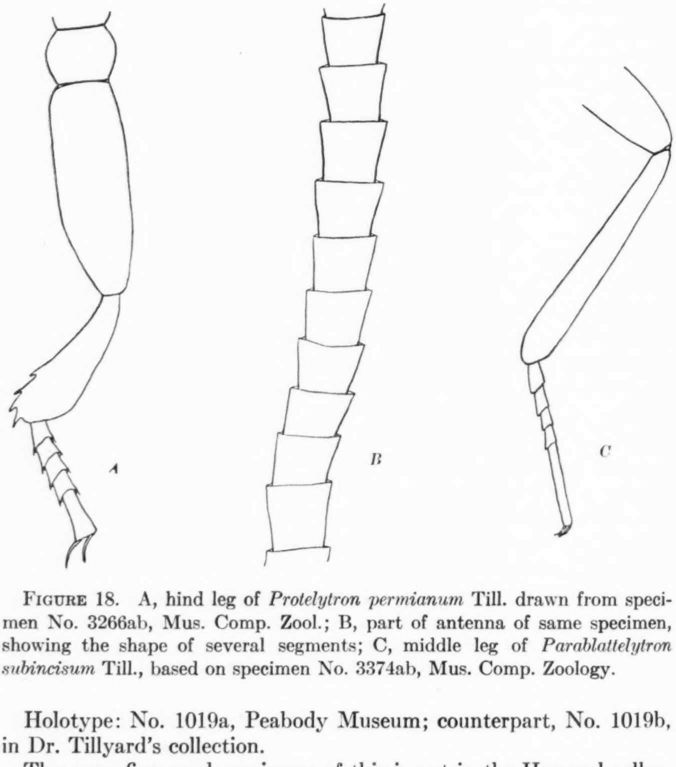

FIGURE 18. A, hind leg of *Protelytron permianum* Till. drawn from specimen No. 3266ab, Mus. Comp. Zool.; B, part of antenna of same specimen, showing the shape of several segments; C, middle leg of *Parablattelytron subincisum* Till., based on specimen No. 3374ab, Mus. Comp. Zoology.

Holotype: No. 1019a, Peabody Museum; counterpart, No. 1019b, in Dr. Tillyard's collection.

There are five good specimens of this insect in the Harvard collection, in addition to numerous poorly preserved elytra which do not merit discussion. No. 3366ab, which was taken in the lower layer

and has already been described above, consists of all four wings and portions of the body; the two elytra are spread out on each side, but one of the hind wings is bent over to the opposite side so that this pair is on the same side of the body. Originally, of course, one hind wing was partly covered by the other, but with the aid of a fine needle I removed all of the uppermost wing and exposed completely the bottom wing. The elytra of this specimen are splendidly preserved and show signs of coloration. Almost the whole costal area is very dark brown and the basal part of the sutural margin is similarly colored. One middle and one hind leg are clearly preserved, as well as the head and one antenna. In all probability the head of this specimen was in a normal position when the insect was entombed, that is, the longitudinal axis of the head was at right angles to that of the thorax, so that the view shown in figure 17 represents the back of the head. This would explain the apparent absence of mouthparts, for the anterior part of the head as preserved in the fossil is really only the anterior border of the vertex. It would also explain the position of insertion of the antennae. Specimen No. 3369ab, lower layer, is a very good elytron, showing the veins distinctly and the hairs with surprising clearness. No. 3370ab, also from the lower layer, is likewise a complete and well preserved elytron, showing the subcosta better than most specimens. No. 3367ab, lower layer, is a fairly well preserved elytron. Specimen No. 3368ab, the only one from the upper layer of limestone, is also a good elytron, though preserved on an uneven surface of the rock.

In two respects the preservation of the elytra of this insect and of the Protelytroptera in general is most unusual. The well-preserved elytra of all fossil Coleoptera and Dermaptera which I have seen, including material from the Florissant, Green River, and Oeningen shales, have distinct indications of the original color of the wing; they are usually uniformly black or brown, or occasionally show some other type of coloration, as maculations. None of the Solenhofen (Jurassic) Coleoptera which I have examined show any color in the elytra, the latter being the same color as the matrix; but these Solenhofen insects are notoriously poorly preserved, which readily accounts for the lack of coloration. The insects of the Elmo limestone, however, are usually very well preserved, the elytra of the majority of the Protelytroptera showing minute spines on the costal area; yet none of them give the slightest indication of ever having been uniformly black or brown. Almost all of these elytra are white like the

matrix, though a few specimens of Protelytron show patches of brown pigment on the costal area. Since the coloration on the wings of many of the Elmo insects is unusually clear (e. g., Dunbaria, Lemmatophora, Agetopanorpa, and the cockroaches), it seems very probable that the elytra of the Protelytroptera were not black or brown, but almost colorless, perhaps yellowish, having at most a patch of brown or black in the costal space.

Another interesting aspect of the Protelytroptera is the actual mode of preservation. Tillyard has already pointed out that when a membraneous wing of an insect is preserved as a fossil, the impression of the upper surface of the wing is the negative of the upper surface in the original wing, so far as the topography of the wing is concerned, that is, the convexity and concavity of the veins. Similarly, the impression of the under surface of the wing is the negative of the lower surface, the topography being like that of the upper surface of the original wing. On the other hand, the surface markings, such as the coloration and hairs, of each surface of the wing is preserved in the corresponding impression, so that any hairs on the upper surface of the wing, for example, are preserved in the impression of that surface, although the topography of that half of the fossil is like that of the under side of the original wing. This situation is obviously due to the structure of the wing, which is essentially in the form of a flattened, hollow sac, the upper and lower surfaces separating as the wing becomes preserved. But apparently as the result of its curvature and thickness, the elytron of the Protelytroptera was not preserved in this manner. An examination of a series of obverses and reverses of these elytra shows that although the surface markings and spines of the upper surface may be visible in the half of the fossil in which the elytron is concave, they are always better preserved in the half containing the convex elytron. Hence, in these elytrophorous insects the half of the fossil which has the topography like that of the upper surface of the elytron also shows the markings of that side. Since it is hardly justifiable to entertain the notion that the spines and coloration were on the under surface of the elytron, I have come to the conclusion that the elytra were more or less replaced by mineral matter during the process of preservation, although enough organic material persisted to effect the limestone chemically, producing a print of the surfaces, analogous to a photographic print, on the exterior. That half of the fossil elytron bearing a concave elytron may therefore be either the mould of the upper surface of the elytron, or

the inner surface of the lower side of the elytron, itself; and the convex half may be either the upper surface of the elytron, or the cast of the inner side. By means of the spines on the costal area it is possible to determine into which category any fossil may belong; if, for example, the elytron is convex and shows the spines, then it is obviously the upper surface preserved. Probably all strongly convex elytra, such as those of most Coleoptera, are preserved in a similar manner. Professor P. E. Raymond, with whom I discussed the matter, informs me that this type of preservation also occurs in the trilobites, in which the external skeleton of the dorsal part of the body was thick and convex.

Protelytron tillyardi, new species.

Figure 19.

Elytron: length, 5 mm.; width, 1.9 mm.; costal area very broad; R straight; R1 slightly arched proximally; Rs arising at about the middle of the wing; M straight, close to R proximally; Cu1 and Cu2 and the anal veins are nearly straight; sutural margin unusually broad.

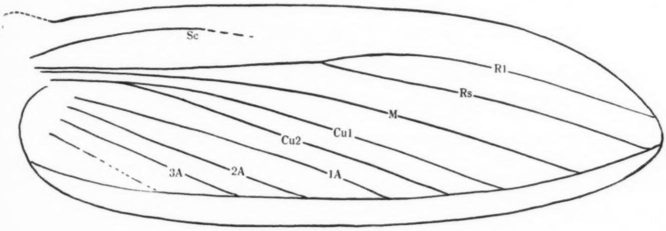

FIGURE 19. *Protelytron tillyardi*, n. sp., elytron; holotype, No. 3372ab, Mus. Comp Zoology.

Holotype: No. 3372ab, Museum of Comparative Zoology; collected by the writer in the lower layer of limestone at Elmo, 1932. The type consists of a complete elytron, with all veins very clear except A2 and A3. This species is distinguished from *permianum* by its proportionally shorter and broader elytron, and by the wide sutural margin. Specimen No. 5405ab in the Peabody Museum, which was designated a paratype of *dunbari*, seems to belong to this species.

Protelytron angustum, new species.

Figure 20.

Elytron: length, 6 mm.; width, 1.8 mm.; costal margin not quite so convex as in *permianum;* apex very pointed; costal area a little narrower than in *permianum;* Sc close and parallel to the costa basally; Rs arising just beyond the middle of the wing; M parallel to R for about one-third the length of the elytron, then diverging away parallel to Cu1; stem of Cu almost touching R at the base; 1A, 2A, and 3A about equidistant; a short anal vein, probably 4A, is visible near the inner angle of the wing; sutural margin very narrow for its entire length, only about one-half as wide as that of *permianum.*

Holotype: No. 3371ab, Museum of Comparative Zoology; collected by the writer in the upper layer of the limestone, in 1932. Although

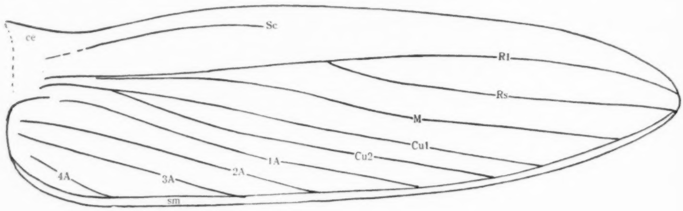

FIGURE 20. *Protelytron angustum,* n. sp., elytron; holotype, No. 3371ab, Mus. Comp. Zoology.

this elytron is about the same size as that of *permianum,* it is distinguished by having a pointed apex, by the submarginal Sc, the presence of a fourth anal vein, and particularly by the narrow sutural margin. The type is very well preserved, except for the very basal part of the costal area, which is broken away as in a great many of the Protelytroptera.

Permelytropsis, new genus.

Elytron: costal margin convex, the costal expansion prominent; Sc strongly developed at the base, terminating on the costal margin just basad of the middle of the wing; Rs arising scarcely beyond the middle of the wing; M arising from the base, free from R or Cu; Cu well developed but unbranched; anal veins not parallel; sutural margin well developed; spines on the costal area and sutural margin at the base.

Genotype: *Permelytropsis cubitalis,* n. sp.

Permelytropsis cubitalis, new species.

Figure 21.

Elytron: length, 6 mm.; width, 2 mm.; apex moderately pointed; costal area very broad; Sc closer to margin than to R, slightly sigmoidal in shape; Rs nearly straight; M sigmoidally curved; Cu strongly convex, diverging away from M at the base, approaching 1A near the middle of the wing, then diverging anteriorly and finally terminating near M; 1A slightly curved away from Cu near the middle of the elytron; 2A remote from 1A basally but converging towards it distally; 3A short, subparallel to 2A; sutural margin nearly the same width for its entire length.

Holotype: No. 3373ab, Museum of Comparative Zoology; collected by the writer in the upper layer of limestone at Elmo, 1932.

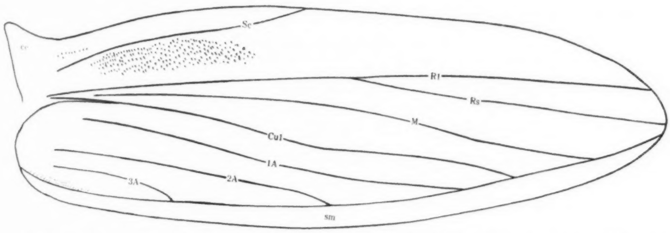

FIGURE 21. *Permelytropsis cubitalis*, n. sp., elytron; holotype, No. 3373ab, Mus. Comp. Zoology.

The outstanding feature of this genus is the unbranched cubitus. It is obvious from the structure of the basal part of this vein that it really consists of Cu1 and Cu2 coalesced; the narrowness of the area between Cu1 and 1A shows that the absence of the branches of Cu is not merely due to lack of preservation. The specimen described is very well preserved, exceptionally so, in fact; the short spines on the costal area, which extend from the base to almost the middle of the wing, are very clear, as well as those at the base of the sutural margin.

Genus *Protelytropsis* Tillyard.

Protelytropsis Tillyard, 1931, Amer. Journ. Sci., **21**: 245; fig. 5.

This obscure genus is known only from a single species (*grandis* Till.) and specimen (No. 5426, Peabody Museum), consisting of

only the very distal end of an elytron. It shares with Megelytron the possession of a faint meshwork of cells, although in Protelytropsis the meshwork is restricted to a much smaller area. The apex of the elytron is more pointed than that of Megelytron. Since only a small fragment of this insect is known, it is not possible to determine its affinities with certainty; the basal part of the elytron, when found, may show features which will require a separate family for this species. Tentatively, however, I believe it fits into the Protelytridae better than into any other described family.

Megelytridae, new family.

Elytron: Sc, R1, Rs, M, Cu1, Cu2 and probably 3 anal veins present; Cu1 apparently branched; costal area broad; no true sutural margin; Rs arising in apical part of wing; distal half of wing with a delicate reticulation.

Genus *Megelytron* Tillyard.

Megelytron Tillyard, 1931, Amer. Journ. Sci., **21**: 247; fig. 7, 8.

This genus is also known from a single species and specimen (*robustum* Till., No. 5406ab, Peabody Museum), no additional representatives having been found in the Harvard collection. The type consists of a more or less whole specimen, with the elytra folded back over the abdomen. I do not believe that a sutural margin is present. In the proximal half of the elytron there is a vein running parallel to the posterior border, forming a margin which superficially resembles the sutural margin, except that it is on the same level as the rest of the wing, and continues the convexity of the elytron as a whole. In the other Protelytroptera the true sutural margin is in the form of a flat shelf. There are apparently no true branches of the main veins, except Cu1, but the distal part of the wing is filled with a meshwork which may have been derived from a complete venational system or may be a secondary formation associated with the development of a coriaceous texture to the wing. Cu1 is probably branched, but even this is not certain, for as Tillyard states the posterior portion of the elytron is covered by the decomposed abdomen. The costal expansion is apparently broken away in the fossil but was probably present in this species as in the others. This fossil is of much interest because it shows a part of the thorax; the prothorax is shaped as I have described it in Protelytron. I do not believe, however, that Tillyard has correctly interpreted the eyes, which he shows as being very small;

only a minute piece of the head is preserved, so that it is not possible to check one side of the head with the other. In the specimen of Protelytron in which I have described the eyes, the whole head is preserved and shows by the symmetry of the parts just what the eyes were like.

Archelytridae, new family.

Elytron: Sc, R1, Rs, Cu2, 1A, 2A and 3A present and unbranched; M present and apparently forked, the anterior branch coalescing with Rs; Cu1 with three long and well developed branches; Cu2 markedly concave, for its entire length; costal area broader than in the Proelytridae; sutural margin well developed. Hind wing unknown.

Archelytron, new genus.

Elytron: costal margin strongly convex, the costal expansion at the base small but distinct; Sc weakly developed at the base, but well formed distally; Rs originating well beyond the middle of the wing; M forked just before the origin of Rs, the anterior branch coalescing with Rs.[17] Cu1 and Cu2 diverging at the very base; Cu1 forking dichotomously near the middle of the wing, the anterior branch forking again before the division of M; Cu2 and the anal veins subparallel and unequally spaced.

Genotype: *Archelytron superbum*, n. sp.

Archelytron superbum, new species.

Figure 22.

Elytron: length, 6 mm.; width, 2 mm.; costal area very broad; apex smoothly rounded; Sc weakly developed at its base; diverging anteriorly and fuses with the costa for a short distance, then gradually leads away and terminating on R1 just about at the origin of Rs; R and R1 straight; M straight up to its point of forking; M3 + 4 terminating at the very end of the sutural margin; Cu2 diverging from Cu1, its point of termination being very remote from that of the latter; 1A close to Cu2, but 2A remote from 1A. The sutural margin is apparently uniform in width for its entire length. There appear to be neither cross-veins nor a meshwork of cells; the entire surface of the

[17] There is of course the possibility that this oblique vein between M and Rs is a modified cross-vein; but I have been led to regard it as a branch of M because it diverges from M at a dichotomous fork, and because it is strongly convex.

elytron is rough and when examined under light parallel with the longitudinal axis of the elytron, a series of short ridges can be seen over the whole surface.

Holotype: No. 3389, Museum of Comparative Zoology; collected by the writer in the upper layer of limestone at Elmo, 1932. The specimen is an observe, splendidly preserved. This species is the most generalized of any of the known Protelytroptera and is the only one in which there are branches on several of the main veins. The phylogenetic significance of this fossil will be discussed later.

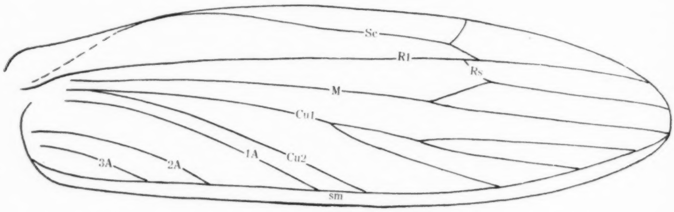

FIGURE 22. *Archelytron superbum*, n. sp., elytron; holotype, No. 3389ab, Mus. Comp. Zoology.

Elytroneuridae, new family.

Elytron: nearly flat, not convex as in the other families of the Protelytroptera. R1, M, Cu1, Cu2, 1A, 2A and probably Rs present and unbranched;[18] 3A absent; Sc present and forked dichotomously before the middle of the wing; R very remote from the costal margin, the costal space being extremely broad; M is fused with Cu1 for some distance basally; Cu2 well developed, markedly concave; sutural margin entirely absent; the short spines already described on the costal space in the Protelytridae are also present in this family.

Hind wing unknown.

Elytroneura, new genus.

Elytron: costal margin strongly convex except at the base; costal space (between Sc and margin) broad, especially at the base of the

[18] Inasmuch as the apical third of the elytron on which this family is based is missing, Rs is not preserved; but since it is present in all other species of the order, it probably existed here as well; and since Rs obviously does not arise before the distal third of the wing it was in all probability unbranched.

elytron, where the margin bulges slightly; Sc well developed, though weak basally; Rs (if present) arising in the distal third of the wing; M fused with Cu1 to about one-third of the length of the elytron; Cu1 and Cu2 diverging away from each other from the base of the wing; Cu2 and the anal veins unequally spaced and not parallel.

Genotype: *Elytroneura permiana*, n. sp.

Elytroneura permiana, new species.

Figure 23.

Elytron: length of preserved part, 9 mm.; width, 3.5 mm.; Sc weakly formed at the base, but apparently arising from near R and arching towards the anterior margin; then curving away just before

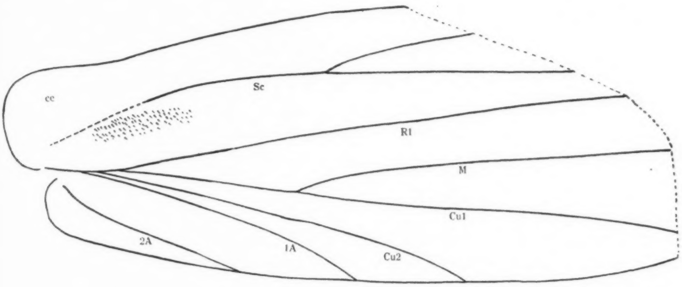

FIGURE 23. *Elytroneura permiana*, n. sp., elytron; holotype, No. 3388ab, Mus. Comp. Zoology.

forking; the anterior fork of Sc is directed obliquely towards the costal margin, the posterior one continuing in almost a straight line the main stem; R strongly developed and nearly straight, directed more or less anteriorly; at the base it is nearer to the posterior margin of the wing than to the anterior margin; M and Cu apparently arising from R at the very base; M and Cu1 straight; M subparallel to R; 1A close to Cu2, 2A remote from 1A; anal area narrowed basally.

Holotype: No. 3388ab, Museum of Comparative Zoology; collected by the writer in the lower layer of limestone at Elmo, 1927. The type specimen consists of a single elytron, minus the apical third, the preserved part of the wing being very clear. The whole elytron was probably about 12 mm. long.

This is one of the most peculiar of all the Protelytroptera. The elytron is distinctly flattened, not convex like that of the other species; yet the wing was obviously hard and coriaceous. In this species the widening of the area between R1 and the costal margin reaches an extreme condition, which together with the narrow anal area produces an unbalanced appearance. The dichotomously forked Sc is probably a primitive feature lost in the other species of the order; but the coalescence of M and Cu1 is a specialization not developed in the others.

Family Blattelytridae.

Elytron: strongly convex; the main veins obsolescent in at least the distal half; anal veins absent; sutural margin well developed. Hind wing: in the genus Acosmelytron, at least, similar to that of the Protelytridae.

Genus *Blattelytron* Tillyard.

Blattelytron Tillyard, 1931, Amer. Journ. Sci. **21**: 250; fig. 9.

This genus includes the single species *Blattelytron permianum* Tillyard, and since that is known only from a poorly preserved fragment of an elytron, it is not possible for us to give as complete a list of the diagnostic characteristics as for the other genera. The base of the elytron being one of the missing portions, the nature of the main veins, Sc, R and M, is not known; it seems almost certain, however, that these veins are weakly developed in the rest of the elytron and simulate those of Parablattelytron. As I have already stated I do not believe that this fossil really lacks the sutural margin, as was thought by Tillyard. The elytron is so badly preserved and so fragmentary that the absence of the margin in the specimen seems almost certainly due to that condition; and under a very oblique light, directed from the posterior border, the faint outline of a sutural margin is, I believe, visible. The type specimen of *permianum* is so poor that I doubt if additional specimens of this species will be recognized. There are no representatives in the Harvard collection so far as I can determine.

Genus *Acosmelytron* Tillyard.

Acosmelytron Tillyard, 1931, Amer. Journ. Sci., **21**: 253.

Elytron: costal margin convex, the costal expansion at the base well developed; Sc, R, and Cu1 are visible at the base of the wing only, Cu1 being more or less straight after its origin; there is no definite Cu2.

Genotype: *Acosmelytron elongatum* Till.

Acosmelytron elongatum Tillyard.

Acosmelytron elongatum Tillyard, 1931, Amer. Journ. Sci. **21**: 253; fig. 12.
Acosmelytron acutum Tillyard, ibid., p. 254.

Elytron: length, 7.8 mm.; width, 2.4 mm. The basal parts of Sc, R, M, Cu1 and even the anal veins are discernible. The sutural margin is broad, more so than in any of the other Protelytroptera. It should be borne in mind that in Tillyard's figure the basal expansion of the costal margin is not illustrated, and that the sutural margin is shown narrowed basally, which is not the case.

Holotype: No. 5415, Peabody Museum. In the Harvard collection there are two fine specimens of this species: No. 3387 and No. 3386ab, both collected by the writer, the former in the lower layer, the latter in the upper layer of the limestone. No. 3386 shows the veins clearly as well as the cluster of spines on the costal space near Sc. *Acutum* was based upon a poorly preserved elytron (No. 5414, Peabody Museum), 7.5 mm. long, but lacking the apex. This fossil shows Cu1 somewhat more clearly than the type of *elongatum*, but this is unquestionably a matter of preservation. In such wings as these, in which the veins are only faintly indicated at best, the degree of perfection of preservation makes a great difference in the appearance of the veins.

Acosmelytron delicatum Tillyard.

Acosmelytron delicatum Tillyard, 1931, Amer. Journ. Sci., **21**: 254; fig. 13.

Elytron: length, 6 mm.; width, 1.6 mm. The type specimen of this species (No. 5416, Peabody Museum) consists of portions of the body and the elytra, fairly well preserved. The fossil may be a small *elongatum*, since there seems to be no differnce except in size. However, the specimen is of much interest since it shows part of the hind leg. In Protelytron, as I have already shown, the hind legs are peculiarly modified and armed; in *Acosmelytron delicatum* they are apparently similar in segmentation and armature. Tillyard has given a figure of part of the leg (fig. 13) but he did not include the complete tarsus, for he did not remove the limestone matrix which covered the four terminal segments. With the permission of the authorities of the Peabody Museum, I removed this matrix and exposed the entire tarsus, which turns out to be like that of Protelytron.

Genus *Parablattelytron* Tillyard.

Parablattelytron Tillyard, 1931, Amer. Journ. Sci., **21**: 251.

Elytron: costal margin convex or at least strongly curved; costal expansion at the base well developed; Sc, R, and Cu2 are visible at the base only, there being no trace of the convex Cu1.

Genotype: *Parablattelytron subincisum* Til.

Parablattelytron subincisum Tillyard.

Parablattelytron subincisum Tillyard, 1931, Amer. Journ. Sci., **21**: 251; fig. 10.

Elytron: length, 7 mm.; width, 2 mm.; slender; R and Cu2 are visible to about the middle of the wing, but Sc can be seen only at the base; sutural margin rather narrow but uniform in width for its whole length; the costal expansion, which is not shown in Tillyard's figure, is shaped as in *Parablattelytron latum*, n. sp. The apex of the elytron is rather pointed, due largely to the curvature of the anterior margin.

Holotype: No. 5401ab, Peabody Museum. The type specimen is not well preserved and a portion of the elytron just distal of the middle of the wing is broken away. In the Harvard collection there are five specimens of this species, as follows: No. 3376ab, consisting of the elytra, parts of the body, and both hind wings; the venation of the latter is not very clear, but enough can be seen to enable us to know that the wing structure is similar to that of the Protelytridae. No. 3377ab, a complete and well preserved elytron. No. 3378, a complete specimen, with the elytra folded over the abdomen; No. 3379ab, a complete and good elytron; No. 3375, also a complete elytron; and No. 3374ab, a nearly complete specimen, the hind wings hidden under the elytra; one middle leg is very well preserved (figure 18c) and shows a rather slender and normal tarsus and tibia; the terminal tarsal segment is as long as all the others combined. Of these fossils, No. 3379ab and 3375 were found in the upper layer of limestone.

Parablattelytron latum, new species.

Figure 24.

Elytron: length, 7.5 mm.; width, 2.8 mm.; very broad; Rs, Cu2 extend to about the middle of the wing; Sc present only at the base; sutural margin broader than in *subincisum;* apex bluntly rounded, the costal margin not so curved distally as in the latter species.

Holotype: No. 3380ab, Museum of Comparative Zoology; collected by the writer in the lower layer of the limestone at Elmo, 1932. This species, which is based upon a complete and well preserved elytron, is readily distinguished by the greater width of the elytron and its bluntly rounded apex.

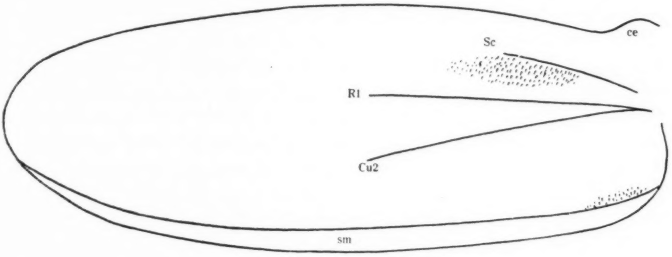

FIGURE 24. *Parablattelytron latum*, n. sp., elytron; holotype, No. 2338ab, Mus. Comp. Zoology.

Parablattelytron rectum Tillyard.

Parablattelytron rectum Tillyard, 1931, Amer. Journ. Sci. **21**: 252; fig. 11.

Elytron: length, 5.2–5.5 mm.; width, 1.5 mm.; Cu2 extending to the middle of the wing; Sc and R present only at the base, R extending a little further than Sc; sutural margin narrow; costal margin and the apex shaped as in *subincisum;* the costal expansion, not shown in Tillyard's figure, is similar to that of the other members of the genus.

Holotype: No. 5413ab, Peabody Museum. In the Harvard collection there are five specimens of this species: No. 3381, 3382, are good elytra, from the lower layer; No. 3384 is a good elytron from the upper layer; No. 3388 and 3383 are poorer elytra from the upper layer. There is one specimen of this species, consisting of an elytron, in the Sellards collection (No. 1417). The elytron of *rectum* is similar to that of *subincisum*, but differs mainly in its smaller size.

THE RELATIONSHIPS OF THE PROTELYTROPTERA.

Tillyard has already presented a very thorough discussion of the possible relationships between the Protelytroptera and the Coleoptera,

and between the Protelytroptera and the Dermaptera. As he points out, this estimation of the affinities of these remarkable insects must be based almost entirely upon the structure of the hind wing, since the fore wings have been reduced along similar lines in all three orders. The conclusion which he reached was that the Protelytroptera had no genetical relationship with the Coleoptera, but were probably ancestral to the Dermaptera; and that the Protelytroptera known to us are a highly reduced remnant of a more extensive group. The new material which has been described in the foregoing pages does not contribute much to our understanding of this particular question. The pentamerous segmentation of the tarsi of the Protelytroptera has no weight in the discussion, for although pentamerous tarsi do occur among some Coleoptera and only trimerous tarsi among the Dermaptera, the pentamerous condition may have been present in the primitive Dermaptera. That this was in fact the case is shown by the Jurassic Dermapteron *Protdiplatys fortis* Mart., from Turkestan, which possessed pentamerous tarsi.

The few changes which I have made in the interpretation of the hind wings of the Protelytroptera do not effect Tillyard's conclusions, for the latter were based not upon the homology of the venation as upon the similarity of folding of the wing in the Dermaptera and Protelytropsis, the condition in the latter apparently representing an elementary stage of folding which has been brought to a higher degree of specialization in the modern Dermaptera. But although I accept Tillyard's conclusion regarding the relationship between the Coleoptera and the Protelytroptera, I believe that more evidence is needed before we are justified in concluding that the Dermaptera are lineal descendents of the Protelytroptera. To my mind there still remains the possibility that the Protelytroptera were an end branch of insects which developed the elytrophorous condition as independently from the Dermaptera as did the Coleoptera; for I am not entirely satisfied that we have certain knowledge of the method of folding of the hind wings in the Protelytroptera. But it is obvious that we know now as much about the structure of the Kansan Permian Protelytroptera as we shall ever know, in so far as the estimate of the relationships of these insects is concerned. New and better specimens may be found, but the facts added will almost certainly be of such a nature as to be unable to contribute materially to our understanding of the phylogenetic position of the order. The evidence to substantiate or to disprove our present views of the affinities of the

Protelytroptera will come when we have a more complete series of insects from the upper Permian and the Mesozoic. Unfortunately, the hind wings of the Jurassic Prodiplatys are folded under the elytra; if we knew the structure of these wings, we would be in a better position to decide more definitely on the relationships of the Protelytroptera with the Dermaptera.

Although the fossils in the Harvard collection do not aid materially in our search for descendents of the Protelytroptera, they do contribute a great deal of information needed in considering the question of the ancestors of these insects. It is clear that so far as the elytra are concerned the order had already attained a long history by the time of the Lower Permian; for the families described above represent several lines of descent which had already reached wide divergence. The hind wings, of course, are not known in enough of the families to enable us to utilize their structural features. But by selecting the more generalized structural characteristics of the elytra in these families, I believe that we can form some idea of the fore wing in the common ancestral group which gave rise to this series of fossils.

We are justified in concluding, I believe, that the evolution of the Protelytroptera as a whole has been in the direction of the perfection of the elytrophorous condition, that is, by the increase of the hardness and convexity, and the atrophy of the venation. That evolution can clearly be seen in the known families. The fore wing in the Elytroneuridae is especially interesting because it is hardly an elytron at all; it is obviously coriaceous and thickened, but it is perfectly flat, not convex as are the elytra of the other families. This type of elytron I consider to represent the more generalized form in the order. The subcosta is shortened, but it is dichotomously forked; this again is certainly less specialized than that of the other members of the order. In all the species R and R1 are unbranched. M is apparently branched in Archelytron, though this branch does coalesce with Rs. In the same genus Cu1 has two dichotomous forks, although in the other species it is unbranched. Cu2 is unbranched in all species; and this is also true of the three anal veins and of the fourth anal vein in *Protelytron angustum*. In Elytroneura the sutural margin is completely absent, and in view of the flattened condition of this wing, I believe that this is a primitive trait. In figure 25 I have included a drawing of a hypothetical wing consisting of the more generalized characteristics. All of the veins, except Cu2 and the basal part of Sc,

are convex, so we are unable to determine whether M is MA, MP, or both combined. This wing bears a strong resemblance both in general form and venation to the fore wings of some fossil cockroaches, in particular those of Scutinoblattina Scudder, Nepioblatta Handl., and Brephoblatta Handl. Scudder called attention in his description of these fossils (1885, 1886) to the pronounced convexity of the fore wings, which are in fact true elytra. The types of these genera are now in the Museum of Comparative Zoology, and on comparing them with specimens of Protelytroptera, I was greatly impressed with the remarkable similarity in the form of the elytra, including the wide costal space, and in the general arrangement of the venation. It is interesting to note in this connection that the elytrophorous condition has apparently arisen several times in the

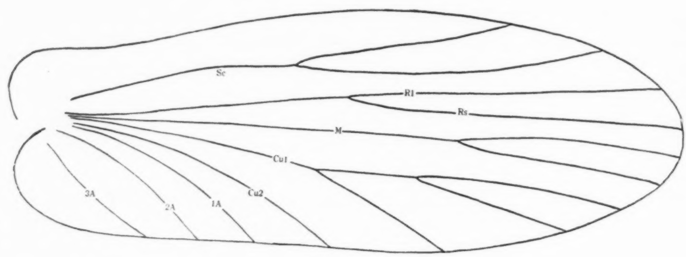

FIGURE 25. Hypothetical elytron of common ancestor of the Permian Protelytroptera; for explanation, see text.

cockroaches.[19] Some of the elytra described by Scudder from the Permian of Colorado and placed by him and Handlirsch in the Blattaria are so close to the elytra of the Protelytroptera that it is not improbable that they may prove to be members of the latter order. I venture to suggest, then, that the Protelytroptera are descended from the ancient cockroaches, probably arising in the lower part of the Upper Carboniferous. Tillyard has already called attention to the resemblance between the Protelytroptera and the insects which he has described from the Upper Permian as Protocoleoptera, and the new fossils described above, especially Elytroneura, serve to intensify this similarity. He suggests that these Proto-

[19] As in the Epilampridae, for example.

coleoptera may prove to be an archaic remnant of the older Protelytroptera, at a stage when the elytron was still tegminous and more or less flat. The family Elytroneuridae, in which the elytra were flat and tegminous, may have been a survival of that very group which was the common ancestral stock of the Protocoleoptera and the more distinctly elytrophorous Protelytroptera.

Order PLECTOPTERA.

The may-flies constitute a very prominent part of the fauna of the Elmo limestone. In the Sellards collection there are nearly forty specimens, of which about a dozen are well preserved. In the Yale collection there are ninety-two specimens, of which one-third were estimated by Tillyard to be in a good state of preservation. In the collection at the Museum of Comparative Zoology there are more than one hundered and fifty specimens, about one-half of which are well preserved. This amounts to a total of more than 280 specimens of may-flies from this single formation. The importance of this fine series of fossils in the study of the geological history and the phylogeny of these insects can be realized if we bear in mind that they constitute the earliest record of true Plectoptera; and with the exception of a single wing from the Permian of Russia and a few doubtful nymphal forms, they comprise the sole representatives of the group prior to the Jurassic.

The specimens in the Sellards collection were studied by Dr. Sellards himself, who published preliminary descriptions of twelve species, based on the best specimens in the material at his disposal (1906). These type specimens I was able to examine and photograph in 1927 in Austin, Texas, although a few of the types could not be found at that time. Unfortunately, a short time after my study of them, all the types were accidently destroyed during the process of renovation of the building in which they were deposited, but the remainder of Sellards collection has been loaned to the Museum of Comparative Zoology. The may-flies in the Yale collection were subjected to an intensive study by Tillyard (1932), who has published a detailed account of his conclusions, together with the descriptions of four new species. These specimens, now at the Peabody Museum, I have also been able to examine.

In his account of the Yale collection Tillyard covered completely certain phases of the phylogeny of the may-flies which consequently require no further discussion. He thoroughly treated the complicated

question of the homology of the veins of the Plectoptera, showing that the evidence provided by these fossils supports in every way the conclusion reached by Lameere in 1922 that the media is represented by both MA and MP, and the cubitus by CuA and CuP. Much of Tillyard's discussion was concerned with an attempt to disprove the view advanced by Martynov in 1923 that the media was only represented by MA; but Martynov had already abandoned that idea and accepted Lameere's, as he states in a paper published in February, 1932, the same month as Tillyard's.[20] In this paper I have therefore employed without change this system of nomenclature.

The conclusions which Tillyard reached on the synonymy of certain of Sellards' genera and species very nearly coincides with those to which I was led in my survey of the types in 1927. But Tillyard was not able to ascertain the differences between the fore and hind wings of these Permian may-flies and consequently he confused certain of these differences with true specific characteristics. Fortunately the new material in the Harvard collection contains specimens which enable us to distinguish satisfactorily between the two pairs of wings. Also, Tillyard was not able to determine much about the body structure of these insects and although he presented a reconstruction of *Protereisma permianum,* his figure is incorrect in many respects and gives an erroneous idea of the habitus of the Permian may-flies. Again we are fortunate in having in the Harvard collection a series of fine specimens which show clearly the body structure of these ancient insects.

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[20] Tillyard's remarks concerning my translation of Martynov's Russian paper are somewhat misleading. He states (1932, p. 100) that it was very unfortunate that I "did not see fit" to include Martynov's figures in the translation; and that I did not realize the importance of having the figures to use in connection with the text. But in the introduction to the translation, I stated that "the twelve figures accompanying the original article are essential for a complete understanding of the problems under discussion"; and also pointed out that the nature of the original figures was such that they would have required retouching before they could have been copied. The publication of the translation without the figures cost me personally not less than a hundred dollars, and the reproduction of the illustrations would of course have greatly increased this amount. I naturally assumed that anyone who was interested in the figures in Martynov's paper and who did not have access to the article in the original journal (Rev. Russe Ent. **18:** 145–174), would secure a copy of the issue containing the paper from the entomological society which published it.

Family PROTEREISMATIDAE.

Protereismephemeridae, Sellards, 1907, Amer. Journ. Sci. **23**: 345.
Protereismidae, Handlirsch, 1919, Denkschr. Akad. Wiss. Wien Math. Naturw. Kl. (96) **82**: 63.
Protereismatidae, Tillyard, 1932, Amer. Journ. Sci., **23**: 237.

Fore wing: elongate-oval in shape, somewhat narrowed basally; costa submarginal, forming an arch at the base of the wing; Sc terminating near the apex of the wing; R1 more or less parallel to Sc; Rs originating from R1 near the base, but almost immediately coalescing with MA for a short distance; Rs with three complete triads; R4 + 5 arising a little proximad of the middle of the wing; MA with a single triad arising also at about mid-wing; MP with a single triad originating proximad of the origin of Rs, occasionally closer to the origin of MA; CuA arising from the stem of Cu at the base of the wing, but directed anteriorly and immediately touching M or joined by a short strut to M; CuA with a well developed triad; CuP unbranched; A1 and A2 arising from a thick chitinous stem, joined to the recurved stem of Cu; A1 without a well defined triad.

Hind wing: similar to the fore in shape and size, being only slightly smaller. The venation is also similar to that of the fore wing, but differs in the following points: the costa is closer to the anterior margin in the hind wing than in the fore; CuA does not approach M at the base as closely in the hind wing as in the fore; the hind wing has a well developed triad on A1; and A1 and A2 arise from a common stem at a point where there is a series of thickened cross-veins.

The general habitus of these insects was more or less intermediate between that of the recent Plectoptera and the Palaeodictyoptera. The head was broad, with large globular eyes in both sexes (apparently), and bearing prominent antennae with 11 subequal segments. The thorax was slender and elongate, the prothorax very broad and flattened, having the appearance of possessing small lateral expansions like those found in many Palaeodictyoptera. The legs were nearly homonmous, the fore pair being only a very little longer (4 mm.) than the others, and this difference may have been confined to the male. The coxa and trochanter were very short, but the femur was long and slender; the tibia a little shorter than the femur; the tarsus longer than the tibia and possessing five segments, the metatarsus being the longest and the fourth the shortest. Small tibial spurs were present and also a single small spine at the distal end of each of the tarsal segments. The tarsal claws were prominent. The

abdomen was elongate in the male and only slightly shorter in the female. Ten segments are visible in the abdomen from above; the terminal filaments were present in both sexes and in the male were at least as long as the abdomen, containing upwards of 40 segments; the genital claspers of the male were very much like those in existing species.

As Tillyard has already pointed out, these Permian may-flies undoubtedly passed through the subimaginal stage characteristic of existing may-flies, for the condition of the wings and of the body resembles that of recent may-flies in that state. The structure of the nymphs of these Lower Permian may-flies is very little known, since no well preserved nymphs have been found in the Elmo limestone. One faintly preserved specimen was taken by the writer in 1927; it shows two long filamentous abdominal setae and the general habitus of the recent nymphs, but most of the body is an obscure mass, probably because the delicate gills were folded or twisted over and across the abdomen. Several specimens of may-fly nymphs have been found in the Permian (Upper) of the Old World and in all probability belong to the Protereismatidae or to related families.

Genus *Protereisma* Sellards.

Protereisma, Sellards, 1907, Amer. Journ. Sci. (4) **23:** 347.
Protereisma, Tillyard, 1932, ibid. (5): **23:** 244.
Protechma, Sellards, 1907, ibid. (4): **23:** 349.
Prodromus, Sellards, 1907, ibid., p. 349.
Bantiska, Sellards, 1907, ibid., p. 341.
Rekter, Sellards, 1907, ibid., p. 349.
Pinctodia, Sellards, 1907, ibid., p. 352.
Mecus, Sellards, 1909, ibid., **27:** 151.

Since this is the only genus of the family, it is clearly defined by the characteristics already given under the family. The genotype is *Protereisma permianum* Sellards.

In this genus Tillyard recognized eight species, of which six were originally described by Sellards and placed by him in four genera. I agree entirely with Tillyard's view that all of Sellards' genera except Misthodotes and Esca are identical with Protereisma. Misthodotes is a valid genus, for which Tillyard erected a separate family. The affinities of Esca are not clear; the species included in the genus was not figured by Sellards and when I examined his collection of types in 1927 I was unable to locate the fossil on which he based his descrip-

tion. Since all of Sellards types have subsequently been lost, this genus will probably remain obscure and perhaps should be regarded as a synonym of Protereisma or dropped from the literature altogether.

The classification of these Permian may-flies is rendered difficult by the variability of many venational features, which were supposed by Sellards to be constant in the species. In his classification of the species of Protereisma Tillyard made use of the relative lengths and breadths of the wings, but he also employed certain venational characteristics which he considered constant in the species. From my study of the specimens in the Harvard collection as well as those in the Peabody Museum, I am convinced that some of the venational characteristics with which Tillyard separated the species are subject to much individual variation also, and that others are merely differences between the fore and hind wings; only one specimen (No. 5427) in the entire Yale collection was complete enough to permit a comparison of the wings and from that he was able to ascertain only that the hind wing was shorter than the fore and had a broader anal area. There are numerous specimens of Protereisma in the Harvard collection which have the bases of the fore and hind wings preserved and which have enabled me to ascertain the differences. Of these fossils the following are the most important: No. 3404, 3405, 3420, all *permianum;* and No. 3414, *arcuatum.* Other specimens, although having only one wing preserved, indicate by the position of its attachment to the thorax whether it is a fore or a hind wing, and so enable further comparison. A careful study of these fossils has revealed the following differences between the fore and hind wings:

1. The costa is closer to the margin of the wing in the hind wing than in the fore wing.
2. R1 and Sc are either fused basally or very nearly fused in the fore wing, but in the hind wing they are decidedly remote from each other.
3. CuP always touches or very nearly touches M at the base of the fore wing, but is remote from M in the hind wing.
4. A1 possesses in the hind wing a well defined triad which is absent in the fore wing.
5. A1, IA, and A2 in the fore wing originate from a strong stem arising from the base of the wing; in the hind wing they arise some distance away from the base of the wing at a chitinous node formed by the partial alignment of two or more cross-veins; between this

node and the base of the wing there is a single stout vein apparently formed by the coalescence of the basal parts of A1, IA, and A2.

Now if we consider the characteristics used by Tillyard to distinguish the species of Protereisma we note that he has employed some of these mentioned in the above list. For example, one of the characteristics used in his key to identify *gracile* is that Sc and R are fused basally; but this is now seen to be a feature common to *all fore* wings, and not present in the hind wings of any species. *Sellardsi* was separated from the others by having CuP practically touch M at the base of the wing, which is a characteristic of *all hind* wings. The variation of certain veins in individuals of a species was considered by Tillyard and he noted that many of the basal connections of the veins were unstable, such as the amount of anastomosis between Rs and MA, the length of the costal brace, and the depth of the forks of Rs and MA. From my study of the entire lot of more than 250 specimens of this family, I am convinced that the following venational features are also subject to individual variation, some of which were used by Tillyard in his classification of the species.

1. The shape of the arch formed by the costal vein varies considerably even in the wings of the same individual.

2. The point of origin of the triad of MP is as variable as that of the triads of Rs and MA; it may arise close to the base, almost below the distal end of the costal vein or near to the first forking of MA; and between these extremes there is a complete series of intermediate conditions, as shown in specimens No. 3404ab, 3408ab, 3409ab, and 3390ab of the Harvard collection.

3. The relative widths of the costal and subcostal spaces do not appear to be constant. The majority of specimens have the costal and subcostal spaces subequal in width or the costal space a little wider; but a few wings have been found in which the subcostal space is the broader. This feature does not, however, appear to be associated with any other characteristics that might indicate specific difference, nor does it appear to be confined to either the fore or hind wing. Specimen No. 5438 of the Yale collection, which has a narrow costal space, is a fore wing, as shown by the structure of CuP and the anal veins at the base; but in the Harvard collection there is a wing (No. 3424ab) which also has a narrow costal area, although it is obviously a hind wing, as indicated by its point of attachment to the thorax. Now if we again consider the characteristics on which Tillyard based the species of Protereisma, we note that one of the chief diagnostic

features of *sellardsi* is that the triad of MP arises close to the base, about the level of the costal brace. But the specimens mentioned above in the discussion of this vein show a complete series of gradations from the extreme condition in the type of *sellardsi* to the more normal one. *Gracile* was characterized as having the costal space narrower than the subcostal, which for reasons given above I consider to be only an individual variation.

In view of the evidence supplied by the new material, then, I believe that the number of species in the genus is even less than supposed by Tillyard. *Latum* Sellards and *insigne* Tillyard are at once separated from all others by their large size, the fore wings being more than 25 mm. long. *Arcuatum* Sellards is distinguished by the arched anterior margin, and *elongatum* Sellards by the small number of cross-veins. The remaining species recognized by Tillyard, i. e., *gracile* Sellards, *minus* Sellards and *sellardsi* Tillyard, are in my opinion identical with *permianum*.

Protereisma permianum Sellards.

Figures 26 and 27.

Protereisma permianum Sellards, 1907, Amer. Journ. Sci. (4) **23:** 348; figs. 3, 4.
Protereisma permianum Tillyard, 1932, ibid. (5) **23:** 247; figs. 5, 14.
Protechma acuminatum Sellards, 1907, ibid. (4) **23:** 349; fig. 8.
Prodromus rectus Sellards, 1907, ibid., p. 349; fig. 10.
Scopus gracilis Sellards, 1907, ibid., p. 352; fig. 12.
Protereisma minus Sellards, 1907, ibid., p. 254.
Protereisma gracile Tillyard, 1932, ibid. (5) **23:** 252; fig. 15.
Protereisma minus Tillyard, 1932, ibid., p. 254.
Protereisma sellardsi Tillyard, 1932, ibid., p. 251; fig. 16.

Length of fore wing, 15–20 mm.; width, 4.8–6 mm.; length of hind wing, 17–19 mm.; width, 4.6–5.7 mm. In the specimens which appear to be imagines the membrane of the wings is hyaline and the cross-veins are distinctly brown; in the wings which apparently belong to subimagines the membrane has a uniformly brown tint. Anterior margin straight, not curving until about one-fourth the wing length from the apex; cross-veins numerous; subcostal and costal spaces usually subequal, occasionally one or the other somewhat broader; origin of IMP usually nearly as far distal as the first fork of Rs, but sometimes arising more distad; CuP strongly waved.

Length of antennae, 4 mm.; width of head, 2.8 mm.; length of head, 1.2 mm.; length of thorax, 5.5 mm.; width of prothorax, 3 mm.; length of fore legs, 24 mm.; length of hind and middle legs, 20 mm.; length of abdomen (small specimen), 16 mm.

The holotype specimen, No. 970, was originally in the Sellards collection and was studied and photographed by me in 1927. Since that specimen has subsequently been destroyed along with the other types, I take this opportunity to designate No. 3405ab in the Harvard collection as the neotype. A second specimen, originally in the Sellards collection, consisted only of the body and was placed doubtfully by Sellards in this species or *latum*. This fossil, which has also been lost, is apparently the one to which Tillyard referred as a paratype.

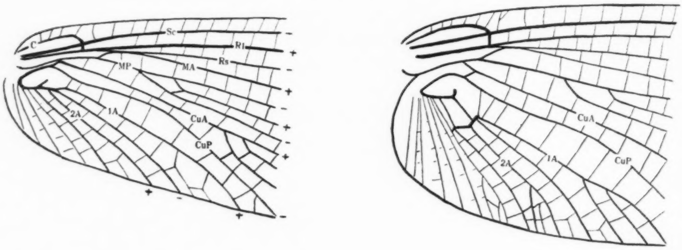

FIGURE 26. *Protereisma permianum* Sell., bases of fore and hind wings, drawn from specimens No. 3404ab, 3405ab, and 3420ab, Mus. Comp. Zoology.

In the Harvard collection there are over forty specimens which can be assigned to this species without question as well as many others which probably belong here. The most important of these fossils are included within the Nos. 3397–3406. Only about a third of the specimens were found in the upper layer of limestone. The restoration of this species, shown in figure 27, is based mainly on the following fossils in the Museum of Comparative Zoology:

No. 3405ab, an excellent specimen, showing the right wings outspread, free from each other, and the two left wings also outspread but slightly overlapping; also showing portions of the body, including one antenna and most of the legs except the tarsi. This fossil shows distinctly the differences between the fore and hind wings.

No. 3404ab, consisting of a fore and hind wing and portions of the body, the legs being especially clear.

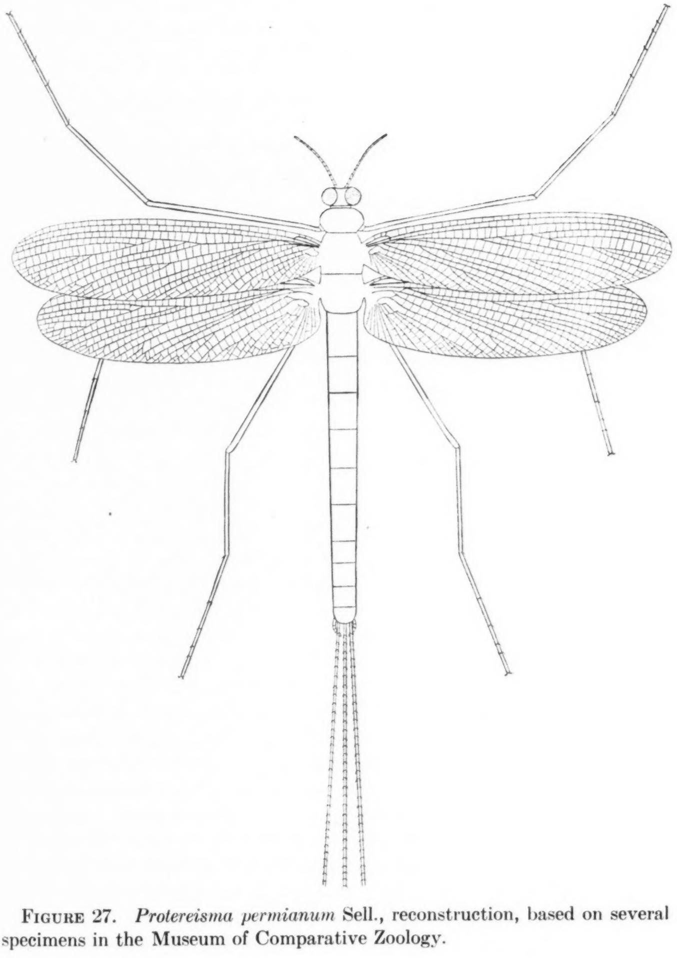

FIGURE 27. *Protereisma permianum* Sell., reconstruction, based on several specimens in the Museum of Comparative Zoology.

No. 3403ab, consisting of the basal halves of two wings and the complete body, showing the antennae and abdomen especially well.

No. 3402ab, a fine lateral view of the whole insect, showing all wings partially overlapped and the legs, including the complete tarsi of two legs.

No. 3400 and 3401, excellent hind wings, showing the anal area unusually well.

Tillyard has already given reasons for synonymizing *acuminatum* and *rectum* with *permianum* and he suggested that *minus* Sellards might also be another synonym. The type of *minus* was somewhat distorted and from my examination of it, I am convinced that the apparent straightness of CuP described by Sellards was due to this distortion. Except for this feature and its slightly smaller size, there are no differences between this wing and that of *permianum*. I have placed *gracile* here also because I believe the characteristics on which Sellards and Tillyard recognized this species were only individual ones. Sellards believed that the wing was distinguished by its slenderness, but this was without definite basis because the posterior part of the wing was missing. Furthermore the apical part of the wing was much wrinkled, as shown by the irregularity of the veins in Sellards' figure; and Sellards himself stated that the wing had suffered "lateral compression," obscuring the radial area at the base. For these reasons, the shape of the type wing cannot be considered as indicative of a similar shape in the species. Tillyard believed that he recognized about a dozen specimens in the Yale collection belonging to *gracile*, which he distinguished by the slenderness of the wing, the fusion of R and Sc at the base, and the broad subcostal space, which was wider than the costal. I have already mentioned above, however, that the fusion of R and Sc at the base is the usual condition if the fore wings of Protereisma, and have pointed out that the relative widths of the costal and subcostal spaces vary even in the same specimen. I therefore regard all specimens in the Yale collection determined by Tillyard as *gracile* to be *permianum*. I have also placed *sellardsi* Tillyard as a synonym of the latter. This species was based upon a single specimen, characterized by having triad of MP arise nearer the base of the wing than in the other species. I have pointed out above, however, that the place of origin of this triad is subject to as much individual variation as the other triads. The species was also based upon the close approximation of CuP and M at the base; but this peculiarity is common to all fore wings of members of the genus, and not confined to any one species.

Protereisma elongatum (Sellards).

Bantiska elongata Sellards, 1907, Amer. Journ. Sci. (4) **23**: 349; fig. 7.
Protereisma elongatum Tillyard, 1932, ibid. (5) **23**: 254.

Hind wing: length, 15–19 mm.; width, 5–5.5 mm.; fore wing probably a little larger. Costal margin straight, curving only in the distal third of the wing; cross-veins fewer than *permianum;* costa (in the hind wing at least) closer to the margin than in *permianum* and other species of Protereisma; CuP markedly waved.

The holotype, No. 976, was present in the Sellards' collection when I studied it in 1927; since it has subsequently been lost, I designate specimen No. 3424ab in the Museum of Comparative Zoology (lower layer) as the neotype. This specimen consists of a fine hind wing and portions of the body. The wing is shown to be a hind wing by the place of attachment to the thorax; it has the same venational features at the base as the hind wing of *permianum.* The basal part of Sc overlaps R at the base, but this is caused by an obvious fold in the wing membrane at this point. I believe that the only definite and constant feature that distinguishes this wing is the smaller number of cross-veins. The proximity of the costal vein to the margin may only be true of the hind wing, but even there it is closer to the margin than in the hind wing of *permianum.* I have not seen any fore wing that can be assigned to this species without question and the specimen mentioned above is the only one in the Harvard material which can be placed here with certainty, though some of the other wings with a more or less open type of venation may belong to this species.

Protereisma arcuatum (Sellards).

Figure 28.

Rekter arcuatus Sellards, 1907, Amer. Journ. Sci. (4) **23**: 349; fig. 6.
Protereisma arcuatum Tillyard, 1932, ibid. (5) **23**: 295; fig. 17.

Length of fore wing, 16–17 mm.; width, 4.7–5 mm.; hind wing a little smaller; costal margin straight for the proximal two-thirds, but curved downwards much sooner than in the foregoing species of the genus; apex pointed; cross-veins numerous; CuP distinctly waved. Tillyard states that the basal part of the anterior margin is strongly curved downward, but that assertion was apparently based upon Sellards' figure, which shows this part of the wing restored in dotted lines. Neither Sellards' specimen nor any specimens in the Yale collection show this part of the wing. In one wing of the Harvard col-

lection (No. 3414ab), however, this region of the wing is preserved and is the same as in the other species of the genus.

The holotype was No. 598 in Dr. Sellards' collection, and was studied by me in 1927; since it is now lost, I designate No. 3414ab in the Museum of Comparative Zoology as the neotype. This fossil, which was collected in the lower layer, consists of the left hind wing, part of the right fore wing and most of the body, including the head, the prothorax, the abdomen and the genitalia. The latter are very well preserved and show that the insect was a male. On the same piece of limestone and only a few millimeters away is a specimen of *Protereisma permianum.* In addition to this specimen there is another representative of *arcuatum,* collected in the upper layer (No. 3413ab); this includes only the apical half of the wing, probably a fore one.

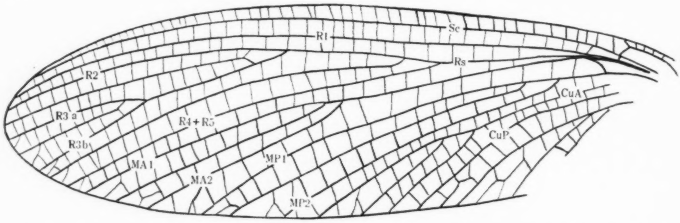

FIGURE 28. *Protereisma arcuatum* Sell., drawn from specimen No. 3414ab, Mus. Comp. Zoology.

Protereisma latum Sellards.

Figure 29.

Protereisma latum Sellards, 1907, Amer. Journ. Sci. (4) **23:** 349.
Protereisma latum Tillyard, 1932, ibid. (5) **23:** 256; fig. 7.

Length of fore wing, 22–25 mm.; width, 6.7–7.5 mm.; hind wing slightly smaller; costal margin straight for the basal two-thirds, distally curved as in *arcuatum;* cross-veins about as numerous as in *elongatum;* anal area of hind wing much broader than in *permianum.*

The holotype was originally No. 124 in the Sellards collection; since that is lost I designate No. 3419ab in the Harvard collection as the neotype; this was collected in the upper layer of limestone.

There are four good specimens of this insect in the Museum of Comparative Zoology: No. 3419ab, the neotype, is an excellent hind

wing, complete and well preserved; No. 3392ab is a complete though somewhat wrinkled hind wing; No. 3391ab, is the basal two-thirds of a fore wing: and No. 3390ab is a fore wing lacking part of the anal area. All of these were collected by the writer in the lower layer, except for the neotype and No. 3391ab, which were taken in the upper layer. This fine species is easily recognized by its large size and relatively broad hind wing. Since the complete wing of this species has not previously been figured, I include here a drawing of the hind wing.

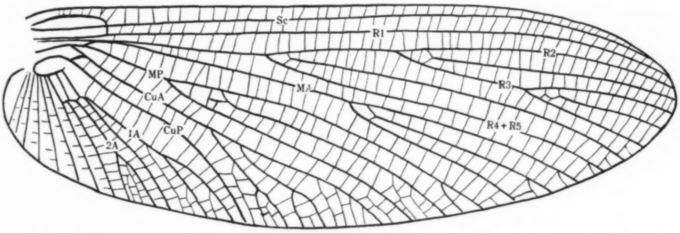

FIGURE 29. *Protereisma latum* Sell., hind wing, drawn from specimen No. 3419ab, Mus. Comp. Zoology.

Protereisma insigne Tillyard.

Protereisma insigne Tillyard, 1932, Amer. Journ. Sci. (5): 259; fig. 18.

Length of hind wing, about 27 mm.; width, 9.4 mm.; fore wing unknown; costal margin straight almost to the very apex of the wing, so that most of the apical curvature takes place in the hind margin, and the apex of the wing is anterior to the longitudinal axis of the wing; cross-veins numerous.

Holotype: No. 1112, Peabody Museum; a hind wing, lacking the distal part.

In the Museum of Comparative Zoology there is one specimen (No. 3436) which I consider to belong here; it consists only of the apical portion of the wing, but it has a width of 8 mm.; and could only fit this species or a new one. The chief feature of this fossil is that the apex is decidedly "off center," that is, above the longitudinal axis of the wing. A comparison of this fossil with the photograph of *insigne* given in Tillyard's paper shows that the outline of the two wings would make a perfect fit, the Harvard fossil including the portions missing in the type. The new specimen was collected in the upper layer of limestone.

Family Misthodotidae.

Fore wing: smaller and relatively broader than that of the Protereismatidae; costa submarginal, but not so strongly developed as in the previous family; Sc terminating on the margin before the apex of the wing; Rs arising from Rs near the base; MA and Rs fused basally, no free part of MA visible; Rs with 3 triads; MP with a single triad; CuA arising from the stem of Cu2 and joined to MP by a short strut, as in the Protereismatidae; CuA without a definite triad, at most with a terminal twig; anal area as in the Proteresimatidae; cross-veins relatively few.

Hind wing: broader than the fore wing, with a more rounded posterior margin; venational like that of the fore wing with the exception of the differences indicated in the Proteresimatidae.

These insects had a shorter abdomen and less elongate legs than the Protereismatidae; the structure of the antennae and tarsi is unknown. The family is much less common in the Elmo limestone than the Protereismatidae, and seems to be absent in the upper layer of the limestone, although additional material may show that it does occur there.

Genus *Misthodotes* Sellards.

Dromeus Sellards, 1907, Amer. Journ. Sci. (4) **23:** 351 (*nec Dromeus* Reiche).
Misthodotes Sellards, 1909, ibid. **27:** 151.
Misthodotes Tillyard, 1932, ibid. (5) **23:** 261.

This is the only genus in the family and consequently needs no further diagnosis. Three species have been described, *obtusus* Sellards (genotype), *biguttatus* Tillyard, and *ovalis* Tillyard. The wings of the latter species are distinguished by their large size, being 15 mm. long; those of *biguttatus* apparently differ from the others by the presence of a color pattern, consisting of two large blotches of brown. Neither of these two species is represented in the Museum of Comparative Zoology.

Misthodotes obtusus Sellards.

Dromeus obtusus Sellards, Amer. Journ. Sci. (4) **23:** 351.
Misthodotes obtusus Sellards, ibid., **27:** 151.
Misthodotes obtusus Tillyard, 1932, ibid. (5) **23:** 261; fig. 19, 20.

Length of fore wing, about 11 mm.; width, 4.3 mm.; length of hind wing, 10.5 mm.; width, 3.9 mm.; costal margin straight, except in the distal region; CuP slightly waved; imago wing without pigmentation.

The holotype specimen of this species was No. 1048 and its counter part 1385 in the Sellards collection; since these have been lost, I designate specimen No. 5470 in the Peabody Museum as the neotype. In the Harvard collection there are two specimens of this insect, No. 3425ab, consisting of a nearly complete hind wing, apparently from a subimago; and No. 3429, the apical part of a fore wing. The Yale specimen mentioned above consists of all four wings and many portions of the body, though details are not visible. Since this is a more complete specimen than either of the two in the Harvard material, I have designated it as the neotype. The various specimens of this species, especially the neotype, show that the fore and hind wings of the members of this family were like those of the Proteresimatidae in general features and differed from each other in the same manner.

Museum of Comparative Zoology,
Cambridge, Mass.

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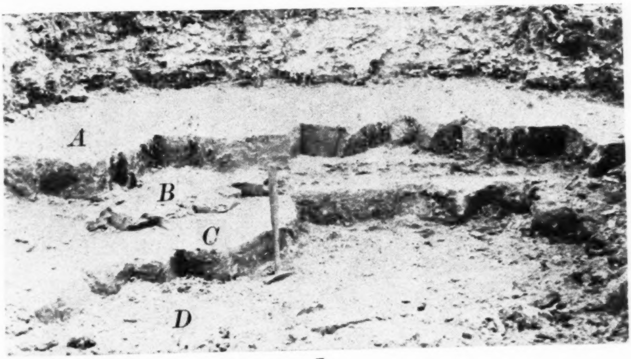
EXPLANATION OF PLATE 1.

FIGURE 1. Photograph of part of the 1932 quarry at Elmo, Kansas. A, upper layer of limestone; B, intervening shale; C, lower layer of limestone; D, top of stump layer.

FIGURE 2. Photograph of head of *Dichentomum tinctum* Till., showing eyes and palpi; specimen No. 3324ab, Mus. Comp. Zoology. Actual length of head, 1 mm. (The dark patches anterior to the eyes are crystals of gypsum.)

FIGURE 3. Photograph of fore tarsi and distal part of tibia of *Dichentomum tinctum* Till.; specimen No. 3348ab, Mus. Comp. Zoology. Actual length of tarsi, 1 mm.

FIGURE 4. Photograph of fore wing of *Delopterum minutum* Sell., specimen No. 5385ab, Peabody Museum, showing the forked Cu1 ($\times$ 20). Photograph by Professor C. O. Dunbar.



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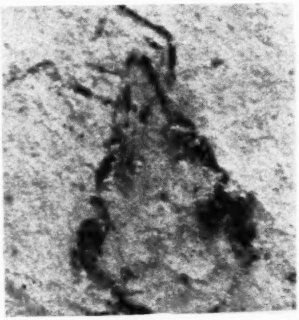

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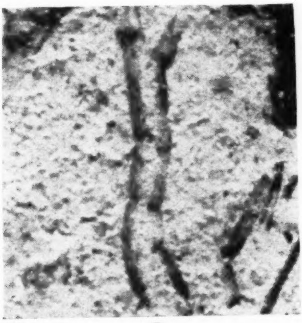

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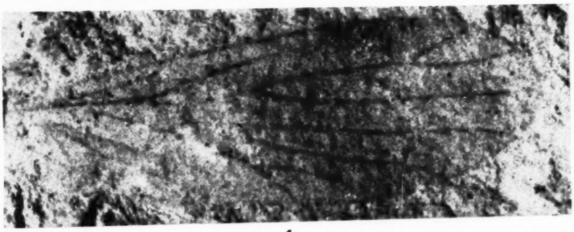

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